Food restriction controls biomass and nutrient fate during growth: insights from a terrestrial consumer

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Consumers circulate nutrients through food webs via resource consumption, growth and waste production. The processes affecting the balance between these three processes at the individual level could scale up to influence ecosystem nutrient fluxes. Here, we quantitatively assessed how food shortage during growth affects the nutrients fate after ingestion. We estimated the balance of eight chemical elements in larvae of *Spodoptera littoralis*. The efficiency of assimilation and retention time of all elements decreased with intake rate. The larvae fed at low intake rates were richer in elements other than carbon, while their waste followed the opposite pattern. Growth efficiency peaked at intermediate rates of both intake and growth. These findings highlight that resource availability controls the balance between element retention and release at the individual level, which should affect trophic dynamics and nutrient recycling at the community and ecosystem levels.

Introduction

Resource scarcity is a common stressor for animals in terrestrial ecosystems, influencing their behaviour, physiology, and survival strategies (Dunham et al., 1989; Karasov, 1986; McCue, 2010; Nagy et al., 1999; Maron et al., 2015). Global change and extreme climatic events are likely to exacerbate the intensity and duration of resource scarcity periods (Johansson et al., 2020; Maron et al., 2015; van Bergen et al., 2020). For instance, drought events can impact herbivore herd population sizes (Godde et al., 2019) or arthropod biomass (Newell et al., 2023), and extreme temperatures can lower the resource quality for juvenile herbivores, which affects their growth (Bauerfeind and Fischer, 2013; DeLucia et al., 2012) and ultimately their demography, population dynamics and communities. Therefore, it is important to study how consumers respond to resource availability to better understand and predict how terrestrial ecosystems will behave in response to global changes.

Consumers, in particular herbivores, can adjust to low food availability in several ways (Sergio et al., 2018). On short time scales, behavioural responses (Scharf, 2016), including expanding food search area, are observed (Abraham et al., 2019). Physiological responses, on the other hand, include reducing nutrient requirements or improving resource use efficiency (McCue, 2010), which results in changes over the fraction of nutrients routed to maintenance, growth, or wastes (faeces, frass, urine etc.). These changes at the individual scale should, in principle, add up and make population and ecosystem-level nutrient fluxes vary as well (Burian et al., 2020). The amount of consumer-driven recycling can partially control primary productivity (de Mazancourt et al., 1998) with potential effects on predator-prey systems (Montagnes and Fenton, 2012), and consumer-plant relationships (Flynn, 2009). Establishing a mechanistic connection between individual growth and nutrient fluxes in a resource-scarcity context requires describing the factors that affect the share between these pathways (Hessen et al., 2004).

In this regard, the efficiencies of two physiological processes – assimilation and growth - are of primary importance. Assimilation efficiency (AE) refers to the proportion of ingested food that is retained within the consumer for growth or maintenance, rather than released as waste. The assimilation efficiency plays an important but overlooked role in nutrient cycles, as it is the fraction of food that is withdrawn from the recycling path of faeces or excretion (Montagnes and Fenton, 2012; Liess et al., 2015; Liess, 2014). As a result, AE plays a critical role in models of fluxes in food webs (Fenton et al., 2010; Montagnes and Fenton, 2012). Growth efficiency (GE), also called conversion efficiency, represents the proportion of consumed food converted into biomass. Higher growth efficiencies result in more material and energy being kept in the food web, and allow more transfer to higher trophic levels and thus sustain longer food chains (Post, 2002; Yodzis, 1984).

Several studies in aquatic settings suggested that AE can decrease at high algae density (Andersen et al., 2009; Fenton et al., 2010; Mitra and Flynn, 2007; Montagnes and Fenton, 2012; Rinke and Vijverberg, 2005). It has been proposed that high algae availability causes high intake rates, which in turn decreases gut passage time and assimilation efficiency (Mitra and Flynn, 2007; Flynn, 2009; Jumars, 2000). But these conclusions may not apply to the terrestrial realm, where marked differences exist with the aquatic realm with regard to the biology of producers and consumers (Burian et al., 2020). In terrestrial systems, the relationship between intake and AE has been reported as negative in isopods and insects (Hubbell et al. 1965; Zheng et al. 1993, respectively), yet as positive or non-significant in other studies on insects (Lawton, 1970). In addition to the discrepancy of these first results, most of these studies did not investigate element-specific efficiencies, which limits the conclusions drawn regarding nutrient recycling. However, it is known from a few aquatic studies that phosphorus and nitrogen assimilation efficiencies can decrease at higher food concentrations, following the total biomass trends (He and Wang, 2007; Kiørboe et al., 1985; Landry et al., 1984; Lombard et al., 2009; He and Wang, 2006). Differences in assimilation efficiency among elements should result in a modification of the ratio of elements in the consumer's body (Hirche and Kattner, 1993; Chen et al., 2005) and wastes, potentially cascading on the rate of element recycling through stoichiometric constraints on the decomposer's optimal substrate ratio (Sterner et al., 2002; Manzoni et al., 2010). By contrast to aquatic systems, variations in consumer recycling path might have strong consequences in terrestrial systems, where the recycling of primary production is much longer than consumer waste due to less decomposable material such as cellulose or lignin (Cebrian and Lartigue, 2004).

To better understand how food availability influences nutrient allocation during growth, we simultaneously measured growth, elemental assimilation, and the chemical composition of both body and waste for eight elements (C, N, P, Na, Mg, S, K, Ca) across a gradient of food intake levels. We tested the hypothesis that resource scarcity would increase the assimilation efficiency of eight chemical elements, possibly to different extents, which, in turn, would increase growth efficiency. We evaluated whether the chemical composition of waste and organisms changed in response to intake levels due to the unequal assimilation of individual elements. We also investigated the

relationship between growth efficiency and growth rate in this resource scarcity context. Our results show that the intake rate affected the assimilation efficiency of elements differently, resulting in changes in the stoichiometry of both body and waste and in a longer retention of nutrients in the biomass. In addition to decreasing at high intake rate due to low AE, GE also decreased at very low intake rate, leaving an optimum of GE at an intermediate intake rate.

Methods

A. Study system

We used the polyphagous Lepidoptera *Spodoptera littoralis* to estimate biomass and elemental balances at the individual level. The measurements were taken during the intense growth period of the seventh and last instar, over which body mass can increase by a factor of four. For the purpose of this experiment, 400 sixth instar larvae from a laboratory strain were isolated in individual 30 mL circular polypropylene containers. Larvae were reared at all times at 25 ℃, 60 - 70% relative humidity, with a 16:8 light/dark cycle (Hinks and Byers, 1976) using a semi-artificial diet whose composition is given in table S1 (76 % water and 43 % C, 4.2 % N and 0.5% P in fraction of dry weight, also see Figure S1). The sixth instar larvae received *ad libitum* food until the start of the seventh instar. The newly moulted seventh instar larvae were then randomly assigned to food availability treatments. At the beginning of the seventh instar, individuals weighed on average 311 $\pm$ 66 mg (mean $\pm$ standard deviation, see Figure S4).

B. Experimental design

We randomly assigned each of the 400 seventh instar larvae to one of five food availability levels (80 individuals per treatment): 120, 240, 360, 480 or 900 mg of food (fresh weight) per day per individual. We had beforehand estimated that the maximal individual intake rate was 595 $\pm$ 43 mg/day/individual, meaning that larvae receiving 900 mg per day were fed *ad libitum*, while the other larvae were not. We conducted this study in ten temporal batches, working with 40 individuals per batch, 8 for each food intake level. We checked that initial larvae masses were not significantly different among the temporal batches (see Figure S2) and among the treatments (Figure S4). Measurements were taken only during active larval feeding and growth. Larvae were fed for two or three days, depending on pre-pupation timing, which varied among treatments and ended measurements due to feeding cessation.

C. Experimental workflow

Throughout the experiment, food was prepared just before each temporal batch and kept in a fridge at 4 °C. Fresh food control samples of every food preparation were kept at -20 °C for subsequent chemical analysis (Figure S1). Every day, each larva was weighed and provided with the assigned quantity of freshly prepared food. We also collected food leftovers and frass daily, promptly stored them at –20 ℃, and later dried them for 72 hours at 60 ℃ in an oven to measure their dry mass. On the seventh instar third day, half the larvae were quickly stored at –20 ℃, dried for 72 hours at 60 ℃ in an oven, and prepared for body chemical analyses. The remaining half was left in the rearing chambers until emergence to examine the impact of food scarcity on mortality, emergence success, and adult body masses. Intake variation did not affect emergence success (only two larvae did not emerge; one was fed 120 mg per day, and the other was fed 900 mg per day). The adult mass upon emergence exhibited a positive correlation with the intake rate during the larval stage (Figure S7).

D. Chemical analysis

To obtain sufficient material for chemical analysis of larvae and faeces, groups of four caterpillars reared under the same temporal block and food provision level were formed. Two individuals were randomly selected for pooled body chemical analysis, while the remaining two were kept alive for estimating emergence rates. Frass chemical analysis was conducted on a composite sample derived from all four individuals.

The dried samples of food, larvae, and frass were ground to a fine powder using a mixer mill (Retsch MM 200). Larvae fat content being high, they were ground after the jar had been plunged into liquid nitrogen. The total carbon and total nitrogen content were determined using an elemental analyzer (Flash HT - Delta V Advantage, ThermoFisher) using aromatic polyimide (EMA-P2) as a standard. The contents of P, Na, Mg, S, K, and Ca were analyzed using ICP-MS after undergoing liquid microwave acid digestion (Milestone 1200 Mega, Milestone Inc., USA) in Teflon bombs with a 3:1 mixture of HNO_3 and HCl.

E. Rates and efficiencies calculations

Dry bodymass was calculated using the larva fresh weight and the larvae water content (average of initial and final larval water content S5). We calculated the average dry bodymass of the individual i over the seventh instar as :

$$b_i = \frac{1}{t_i} \int_{t_i} S_i(t)\, dt$$

where $S_i(t)$ is a smooth growth curve. $S_i(t)$ is a natural cubic spline fitted independently for each individual. t_i is the number of days spent in the seventh instar before pre-pupation by individual i ($3 \leq t_i \leq 4$).

Mass-specific intake rate (MSIR) given in mg of food · mg of individual $^{-1}$ · day $^{-1}$ is computed as:

$$\text{MSIR}_i = \frac{I_i}{t_i b_i}$$

with I_i the total mass of food ingested by the individual i throughout the seventh instar, in dry weight (DW). In the case of a group of caterpillars used for chemical analysis, the corresponding mass-specific intake rate is computed as the arithmetic mean of individual MSIRs.

Growth rate (GR_i) is computed over the seventh instar as the growth average divided by the bodymass of i:

$$\text{GR}_i = \frac{\ln(b_{i,f}) - \ln(b_{i,0})}{t_i}$$

With $b_{i,f}$ the final bodymass and $b_{i,0}$ the initial body mass of i. GR is given in mg of growth (DW) · mg of body (DW) $^{-1}$ · day^{-1}

Assimilation efficiency (AE) is the proportion of ingested mass which is subsequently not egested nor excreted, over the seventh instar, given here in % DW, by:

$$\text{AE}_i = \frac{I_i - E_i}{I_i}$$

with E_i the total dry mass of frass produced by the individual i throughout t_i. AE is a dimensionless quantity (mg of assimilation · mg of food eaten $^{-1}$). Elemental assimilation efficiencies are computed at the level of a group of 4 caterpillars as

$$\text{AE}_{x,k} = \frac{I_{x,k} - E_{x,k}}{I_{x,k}}$$

with $I_{x,k}$ the total intake of element x in group k and in $E_{x,k}$ the total frass mass of element x in group k.

Growth efficiency (GE) is the fraction of ingested food resulting in mass increment:

$$\text{GE}_i = \frac{\Delta b_i}{I_i}$$

with Δb_i the change in dry body mass over t_i. GE is also a dimensionless quantity (mg of growth · mg of food eaten $^{-1}$).

Retention time (RT), the average time an element spends in the body pool, was computed by dividing the pool of the element in the bodymass by the output rate of the element:

$$\text{RT}_{xk} = \frac{b_{x,k}}{E_{x,k}}$$

with $b_{x,k}$ the average pool of element x in group k, and $E_{x,k}$ the average mass of element x egested by larvae of the group k throughout the duration of the seventh instar.

As a whole, we were able to measure body mass, growth rate, growth efficiency, total assimilation efficiency, and body chemical composition at the individual level ($n = 80$ per treatment; $n = 400$ in total), while frass chemical composition and elemental assimilation efficiency were measured at the level of groups of four caterpillars ($n = 10$ per treatment; $n = 100$ in total).

F. Statistical analyses

Due to non-linearity, we used generalised additive models (GAMs) to describe the relationships between mass-specific intake rate and growth rate, absorption efficiencies (including at the element level), growth efficiency and element retention times . Except for two models (GE ~MSIR and GE ~GR), for which we use adaptive splines, all models operated under thin plate regression splines (Wood, 2003). Models diagnostics suggested the use of different families for the conditional distributions of the response variables. Scaled Student's t distributions were used for GR and GE when being used as the dependant variable. We used the gamma distribution and the log link function for retention times, a Gaussian family for larvae and frass element content, and a beta distribution with logit

link function for absorption efficiencies. Models were fitted using the mgcv package in R (Wood, 2017).

Before fitting the models mentioned above, we removed outliers by using a very conservative threshold of leverage given by:

$$h_{ii} < \frac{10p}{n}$$

where h_{ii} is the leverage value of the observation i, p the number of parameters, and n the number of observations. A much lower threshold of $2p/n$ is sometimes used. We did not use Cook's distance because it does not have the same properties in the generalized linear model case as in the linear model case. For each model, the final N is available in the supplementary information.

The first derivative as well as the associated simultaneous confidence interval were computed using the gratia package in R (Simpson, 2024). This allows to determine whether the slope of the smooth at any particular predictor value is significantly positive or negative.

Finally, we fitted two generalized additive models (GAM) with the appropriate family and link function (see above) including the elements as a factorial predictor and the mass-specific intake rate (MSIR) as a continuous predictor: one with assimilation efficiency (AE) and the other with retention times (RT) as dependant variables. We used GAM predicted means to determine whether AE and retention times RT differed between pairs of elements. Additionally, we used these GAM's slopes to probe differences in the relationship between mass-specific intake rate (MSIR) and both AE and RT among different elements, using the marginaleffect package in R (Arel-Bundock et al., 2024).

Results

G. Effects of intake on total assimilation and growth efficiencies

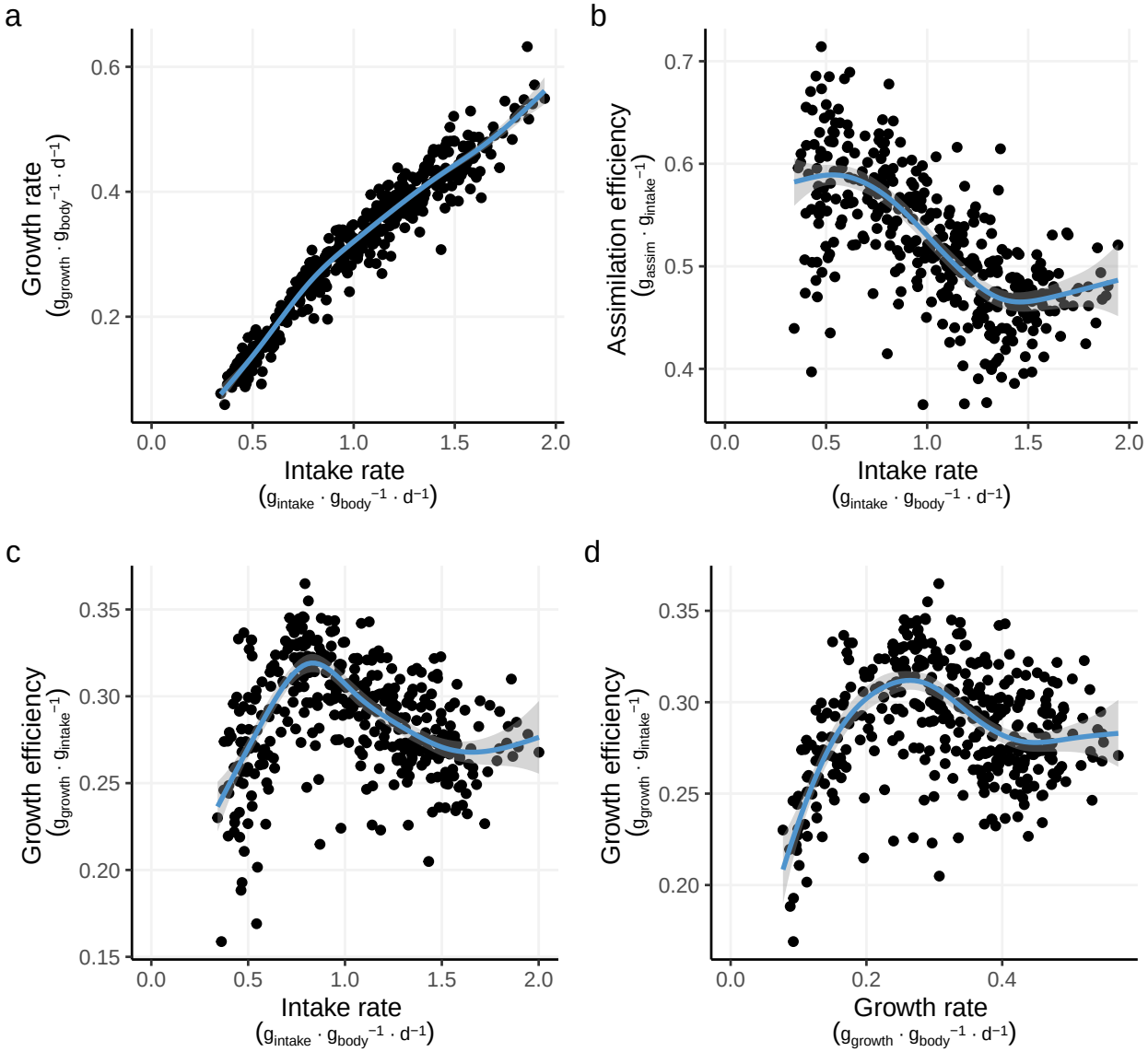

Figure 1. Relationships between intake (MSIR), growth and total assimilation. One point represents a measurement taken at the level of one individual ($n = 400$). All variables are on a dry weight basis. The lines represent GAMs, and shaded areas are 95% confidence intervals of the mean. Models details are given in table S2.

Intake rates varied among individuals within each of the five food provision treatments, resulting in a gradient of mass-specific intake rates ranging from 0.34 to 2.03 $g_{intake} \cdot g_{body}^{-1} \cdot day^{-1}$. As expected, growth rate exhibited a positive relationship with intake rate, (Figure 1a, Figure S6a). Assimilation efficiency decreased non-linearly with intake rate and was thus higher for underfed individuals (Figure 1b, Figure S6b). On average, underfed individuals had an assimilation efficiency of 60%, whereas well-fed individuals were around an efficiency of 45% (Figure 1b).

The relationship between growth efficiency and intake rate (Figure 1c), as well as the relationship between growth efficiency and growth rate (Figure 1d), were non-monotonic, first increasing, then decreasing. The first derivatives for these models indeed show that the slope is significantly positive before becoming significantly negative (Figure S6c and d). The highest growth efficiency (32 %) was observed at an intermediate intake level (0.8 $g_{intake} \cdot g_{body}^{-1} \cdot day^{-1}$) and intermediate growth rate (0.26 $g_{growth} \cdot g_{body}^{-1} \cdot day^{-1}$)

H. Impact of intake level on element assimilation and retention time

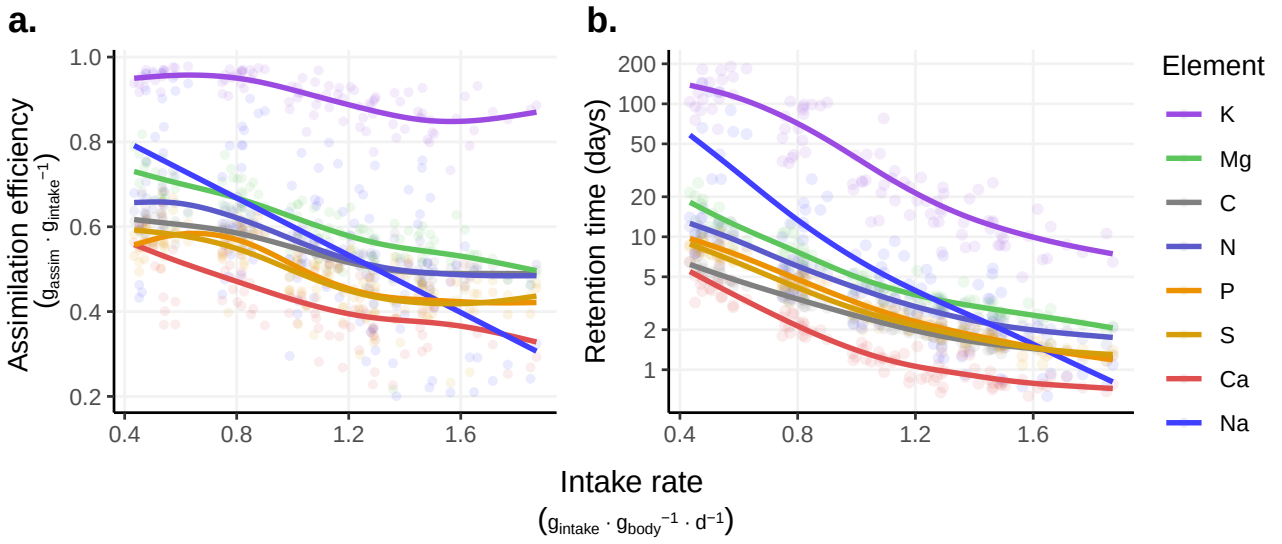

Figure 2. Assimilation efficiencies and retention times for each of the eight elements (C, N, P, Na, Mg, S, K and Ca) according to intake rate (MSIR computed at the level of a group of 4 caterpillars; $n = 100$). Retention time is the average time an atom of the element spends within the larva before being egested or excreted. Lines show GAMs. Models details are given in table S3.

The assimilation efficiencies (AEs) of all elements examined here decreased with intake rate (Figs. 2a and see also figs S8 and S9). However, both the overall AEs and the strength the effect of intake differed among elements, as reflected by the varying average predictions (table S4) and slopes of these relationships (table S5). Considered in pairs, almost all combinations of elements exhibited significant differences in the average AEs over the range of intake rate (except the pairs C-N, P-S, and Na-Mg (table S4)). The effect of intake on AEs also differed between some pairs of elements, including most pairs involving Na or K (table S5). Interestingly, the effect of intake on AE did not differ between C, N and P. There was no obvious peak in elemental assimilation efficiencies at intermediate intake rates (Figure 2a).

Similarly to AE, the retention time (RT) of all elements strongly decreased with intake rates (Figs. 2b, S11). The RTs of elements all significantly differed from each other (table S6). Reducing the intake to the minimum tested here doubled the RT for C, multiplied it by five for N and P, and by 50 for Na. The effect of intake on RT also varied between most pairs of elements, except for C-Ca, N-P, and P-S.

I. Impact of intake rate on body and wastes CNP composition

Larvae feeding at high intake rates were generally richer in carbon, whereas larvae feeding at low intake rates were richer in N, P and the other elements (Figure S12). As a result, body C/N and C/P ratios increased with intake rate (Figure 3a and b). However, intake restriction yielded uneven levels of enrichment for different body nutrients, including N and P, which resulted in body N/P ratio increasing with intake rate (see Figure 3c).

At low intake rates, frass was poorer in virtually all measured nutrients (Figure 3 and Figure S13), suggesting that O and/or (which were not measured) would vary as well. Not all nutrients were equally rarefied in frass as a result of low intake. For instance, frass N/P ratio increased with intake rate (Figure 3f). Of interest is the positive, although weak, relationship found between body N/P and frass N/P (Figure S15).

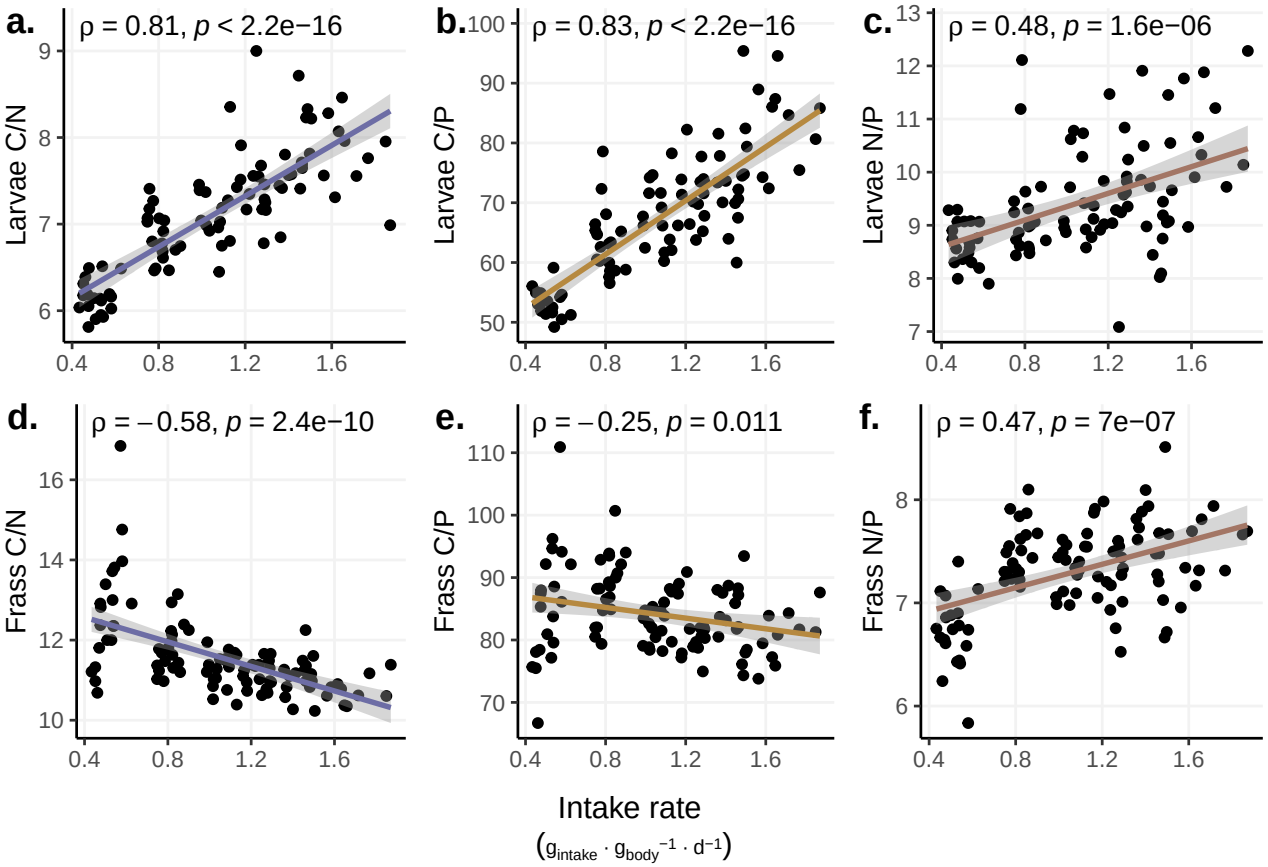

Figure 3. Effect of intake rate on body and frass chemical composition illustrated through the massic ratios between C, N and P. Each point is a measure done with pooled samples of 4 individuals for frass and two for larvae ($n = 100$). The lines represent linear models. ρ is the Spearman correlation coefficient, and the p-values are those of the associated correlation tests.

Discussion

Our study provides a comprehensive analysis of mass and elemental fluxes in a terrestrial herbivore across varying levels of food availability during growth. We found that reduced food availability led to higher elemental assimilation efficiency, extended nutrient retention times, increased nutrient content within consumers (other than C), and decreased nutrient content in waste. Moreover, mildly reducing intake rate increases growth efficiency, whereas further decreasing intake rate lowers growth efficiency again. These findings suggest that food availability can impact trophic transfer efficiency and nutrient cycling in terrestrial foodwebs through physiological adaptations in growing consumers.

J. Assimilation efficiency increases with food restriction

The higher assimilation efficiency at low intake rates in our terrestrial consumer is in line with numerous studies in aquatic species (Gaudy, 1974; Landry et al., 1984; Besiktepe and Dam, 2002; Kiørboe et al., 1985; Thor and Wendt, 2010). This trend has been interpreted as a result of longer gut transit times at low intake, passively lengthening digestion and absorption time, thereby increasing assimilation efficiency (Mitra and Flynn, 2007; Flynn, 2009; Jumars, 2000). The same process is probably at play here. However, other studies, both in aquatic and terrestrial species, found positive or no correlation with intake rate (Lawton, 1970; Conover, 1966; Barthel, 1983; Besiktepe and Dam, 2002). Interestingly, modelling approaches suggest that the theoretical relationship between intake rate and absorption efficiency, while always negative, can change in intensity as a function of food quality (Burian et al., 2020; Mitra and Flynn, 2007), with slopes being close to 0 in certain situations. This may explain the absence of effects observed in some studies.

K. Growth efficiency peaks at moderate food restriction and growth rate

Growth efficiency exhibited a non-monotonous response to intake rate, and hence to growth rate. Starting from *ad libitum* levels, decreasing the intake raises growth efficiency, supposedly as a result of increased assimilation efficiency. Further decreasing the intake, however, reduces growth efficiency. This likely reflects a diversion of resources toward constant and obligatory maintenance processes, involving respiration, rather than growth (Wang and Post, 2012; Pirt and Hinshelwood, 1965). Previous studies have reported both positive (Liu and Ban, 2016; Pandian, 1967; Wang et al., 1998) and negative (Straile, 1997; Lukas and Wacker, 2014; Paffenhofer, 1976; Mullin and Brooks, 1970; Bartley et al., 1980) relationships between food availability and growth efficiency. Some studies, although rare, also suggest a non-monotonic relationship (Urabe, 1991; Urabe and Watanabe, 1991; Reeve, 1963). The absence of non-monotonic relationships in most previous studies may stem from the limited ranges of resource availability examined, which may have coincidentally captured only the monotonic portions of the underlying relationships. Overall, our results indicate that growth efficiency is maximised at intermediate values of intake rate and growth rate.

In the context of trophic transfer, this suggests that there is an intermediate food availability level associated with the maximal trophic transfer efficiency, but with an intermediate trophic transfer rate. Such a response to resource availability might have consequences at the population or community level. Limited availability of basal resources may cascade through food webs, slowing but increasing the efficiency of energy transfer at each trophic level (Fenton et al., 2010; Montagnes and Fenton, 2012). This could mitigate declines in trophic transfer fluxes, thereby helping to maintain food chain length under conditions of resource scarcity (Post, 2002). Some theoretical studies have incorporated the negative relationship between assimilation efficiency and food availability in predator-prey models and found qualitative differences in dynamics (Montagnes and Fenton, 2012; Li and Montagnes, 2015; Mitra and Flynn, 2007; Burian et al., 2020) and higher predictive power (Fenton et al., 2010; Montagnes et al., 2019). However, popular models of ecosystem management, such as Ecopath, Ecosim (Christensen and Walters, 2004) or the Madingley models (Harfoot et al., 2014), do not currently incorporate variations in assimilation or growth efficiencies. Integrating this additional complexity is likely to enhance their effectiveness as tools for management and conservation, while also deepening our fundamental understanding of food web dynamics.

L. Response of assimilation efficiency to intake rate differs among nutrients

Larvae exhibited higher nutrient assimilation at low intake rates across all eight chemical elements. However, the overall assimilation and the effect of intake on assimilation varied among elements (Figure 2). Overall, this suggests that food restriction uniquely influences the retention of individual elements in biomass as well as the stoichiometry of assimilation and egestion fluxes (table S7). The differences in assimilation among elements could be interpreted in two non-exclusive ways: either the relative requirements of elements change with intake level and assimilation is

regulated to reach an objective balance; or the assimilation cannot be improved in the same way accros all nutrients, and this may depend on their molecular context. Indeed, some minerals exist as free ions (K, Na, Ca) and are readily absorbed through channels and pumps in the gut (Rajendran et al., 2018). In fact, our data suggest that 90 % of the K and 70 % of the Na are assimilated at low intake rates (Figure 2). However, an increase in intake rate drastically reduces the assimilation of Na, and Ca is poorly assimilated at all intake rates (Figure 2). Steep slopes for some of these cations, whose concentrations are crucial in maintaining chemical osmosis and appropriate signalling (Bradley, 2009; Clapham, 2007; Naikkhwah and O'Donnell, 2012), might suggest a rather constant requirement that does not increase with physiological changes happening at higher intake (*e.g.* growth). By contrast, other elements known to be crucial to biomass construction occur in complex molecular contexts, such as C, N, P and S, which are found in proteins, carbohydrates, nucleic acids and phytates. Some of these compounds are refractory to digestion, (*e.g.* complex carbohydrates, phytates (Martin, 1983; Huang et al., 2009)), and this may hinder the proper assimilation of these elements at low intake rates, leading to decreased growth efficiency. Molecular biology experiments would be necessary to properly disentangle how changes in physiological requirements and adaptive mechanisms of assimilation combine in the response of nutrient assimilation to food restriction.

M. Food restriction increases retention times

Low intake resulted in longer retention times of nutrients in the body pools (Figure 2). As a consequence, at low intake, the larvae transiently immobilised nutrients that would have otherwise been more rapidly voided as frass at higher intake rates. This suggests that at the ecosystem scale, low-productivity environments (such as tundra and deserts) or temporary disturbances that reduce productivity can result in consumers retaining nutrients for longer periods. This could potentially contribute to slowing down the nutrients cycling rate of nutrient-poor ecosystems - where cycles rates are already low - (Delgado-Baquerizo et al., 2013) and lead to a reduction in productivity in a negative feedback loop (Pastor et al., 1993). In theoretical studies, the return of nutrients through egestion and excretion has been shown to have a small but positive effect on recycling in nutrient-poor systems (Cherif and Loreau, 2013). However, if retention times are lengthened in these situations, this positive effect might be attenuated. This only holds, however, if the consumers' lifespan is not shortened by food restriction, which would speed up recycling by returning more frequently - through death - the nutrients contained in the consumers' bodymass. Several experiments show that moderate food restrictions instead extend lifespan (Partridge et al., 2005; Speakman and Mitchell, 2011), and should, in this context, trigger a longer retention of nutrients in consumer biomass.

N. Food restriction modifies body and waste stoichiometries

As a result of modified assimilation efficiencies, the elemental composition of both larvae and their frass was also impacted by intake rate. At high intake rates, the body nutrient content was lower apart from C (Figure 3a and b). This was due to the accumulation of C, supposedly in the form of fat, at high intake. Similarly, the N/P ratio of larvae increased with intake rate (Figure 3). The variability in consumer stoichiometry has been mostly interpreted as originating from resource stoichiometry variability (Persson et al., 2010; Simpson et al., 2002; Persson et al., 2010; Hessen et al., 2013; Wei et al., 2022). However, our data suggests that not only does resource quality influence consumer stoichiometry, but the resource supply rate as well. In an ecological context, the variation in the carbon-to-nutrient ratio in consumers has been shown to shift the limiting nutrient in secondary consumers (Elser et al., 2016; Jensen et al., 2011; Schoo et al., 2010). It suggests that resource availability could affect not only the flux of biomass between trophic levels, but also the stoichiometry of these fluxes up to the secondary consumer (Boersma et al., 2008, 2009; Malzahn et al., 2010). The level of nutrients in frass also varied with intake rate (Figure 3c and d, Figure S12). At low intake rate, waste was produced in low quantity and quality. Low nutrient content is known to reduce the decomposition rate (Zechmeister-Boltenstern et al., 2015; Enríquez et al., 1993; Güsewell and Gessner, 2009; Wang et al., 2018; Sitters et al., 2014), slowing down even more the cycling of nutrients at low intake. The waste N/P ratio decreased at lower intake, suggesting that N was poorly excreted, while P, found mainly in egesta, continued to be egested, potentially due to the poor digestibility of phytates (Yang et al., 2022).

Resource quality has repeatedly been highlighted as a primary factor affecting nutrient cycling by consumers (Sterner et al., 1992; Elser and Urabe, 1999; Sterner, 1997). The physiological adaptation consisting of preferably retaining the limiting nutrient and releasing non-limiting ones has been shown to have effects on nutrient cycling at the ecosystem scale (McManamay et al., 2011; Andersen et al., 2005; Atkinson et al., 2017; Dalton et al., 2017). An increasing number of studies have now described the effects of physiological adaptation to changes in food quantity (Mitra and Flynn, 2007; Burian et al., 2020). Our work suggests that ecological communities might respond to food shortages by compensating for the scarcity of food with an uneven rise in the trophic transfer efficiencies of main nutrients, associated with the lengthening of nutrient sequestration in biomass. Moreover, both the stoichiometry

of the consumer and of its waste might change as a result of food shortage, potentially influencing the limiting nutrients of both the autotroph and the secondary consumer. Finally, at extremely low food availability, most material is devoted to maintenance with an associated decrease in growth efficiency.

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Supplementary Information

The following figures and graphs provide details of the methods (table table S1 and Figure S2, Figure S4) and some supplementary results. You will find the ingredients (table S1) and the measured elemental composition (Figure S1) of food. The fresh body mass of larvae at the onset of the treatment period is given for each week of the experiment in Figure S2. As growth rate is dependent on initial body mass, it was essential to make sure that starting body mass was overall similar among temporal blocks. Despite small variations, all larvae were in the same larval stage (L6), ensuring an overall similar growth pattern. The assimilation of elements provided in the main text Figure 2 are shown in separate panels in Figure S8 showing for all elements, an increase of assimilation at lower intake. The details of body and frass elemental compositions are shown in Figure S12 and Figure S13, respectively. Larvae C content is increased at higher intake, whereas all other nutrient contents are decreased. All measured nutrient contents are decreased at lower intake in the frass, suggesting an increase of either O or H at low intake (not measured). The relative content of each element in food, body and frass is shown in Figure S1. Body is richer in all elements but Ca at low intake.

Methods

In this section, we describe the food composition (table table S1), and also its chemical analysis along with that of frass and larvae (Figure S1). The variation of the initial fresh body mass among the temporal blocks is shown in Figure S2 and among the food level treatments in Figure S4. We also show how the water content, used to compute various variables on a dry weight basis, evolved during the experiment and between groups in Figure S5.

Ingredient	**Mass fraction % m/m**
Deionized water	76.7
Soja meal	6.79
Corn flour	6.79
Germalyne	3.40
Yeast	2.55
Agar	1.20
Casein	7.19E-01
D-Glucose	6.01E-01
Ascorbic acid	5.10E-01
Benzoic acid	2.69E-01
Linseed oil	1.92E-01
Nipagin	1.16E-01
Choline chloride	5.41E-02
Formaldehyde	3.60E-02
Alpha-Tocopheryl acetate	1.59E-02
Actitetra (Oxytetracycline 50$\%$)	9.59E-03
Ampicillin sodium salt	7.19E-03
Myo-inositol	3.61E-03
Nicotinic acid	3.21E-03
Menadione	1.62E-03
Retinyl acetate	1.30E-03
Riboflavin	7.21E-04
Pyridoxine	7.21E-04
Thiamine hydrochloride	7.21E-04
Ergocalciferol	9.02E-05
Folic acid	6.49E-05
Biotin	1.44E-05
Cobalamin	9.74E-07

Table S1. Composition of food distributed to larvae in mass fraction. Ascorbic acid is vitamin C, Nipagin™ is a broad-spectrum antimicrobial agent. Alpha-tocopheryl acetate is a vitamin E acetate. Oxytetracycline is a broad-spectrum tetracycline antibiotic. Nicotinic acid is a vitamer of vitamin B_3. Menadione is a vitamin K_2 precursor. Retinyl acetate is a form of vitamin A. Riboflavin is vitamin B_2. Pyridoxine is a form of vitamin B_6. Thiamine is vitamin B_1. Ergocalciferol is vitamin D_2. Folic acid is vitamin B_9. Biotin is vitamin B_7 or vitamin H. Cobalamin is vitamin B_{12}.

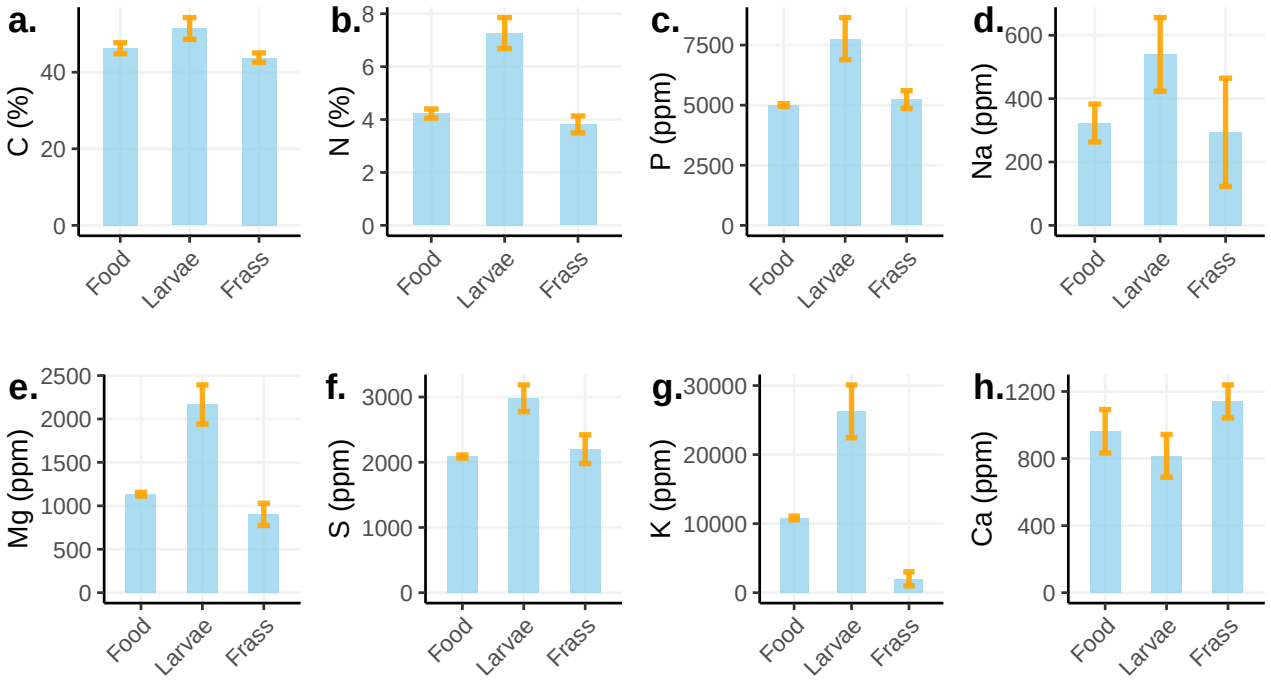

Figure S1. Differences in content between food, larvae (all conditions) and frass in the eight elements.

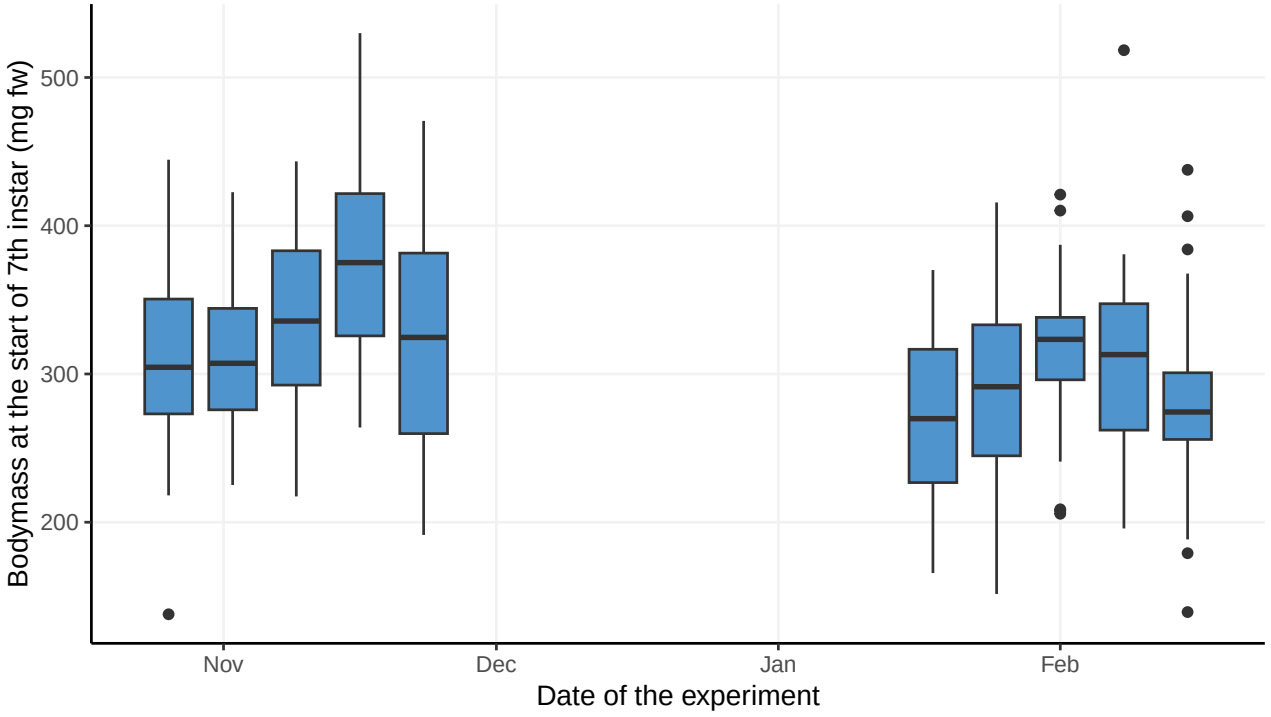

Figure S2. Variation of larvae fresh body mass at the start of the experiment among the ten weeks of work (years: 2021-2022). Each point represents an individual. At the start, larvae are at the very beginning of their seventh larval stage. Only one week (4) shows a slightly higher body mass than the expected 300 mg.

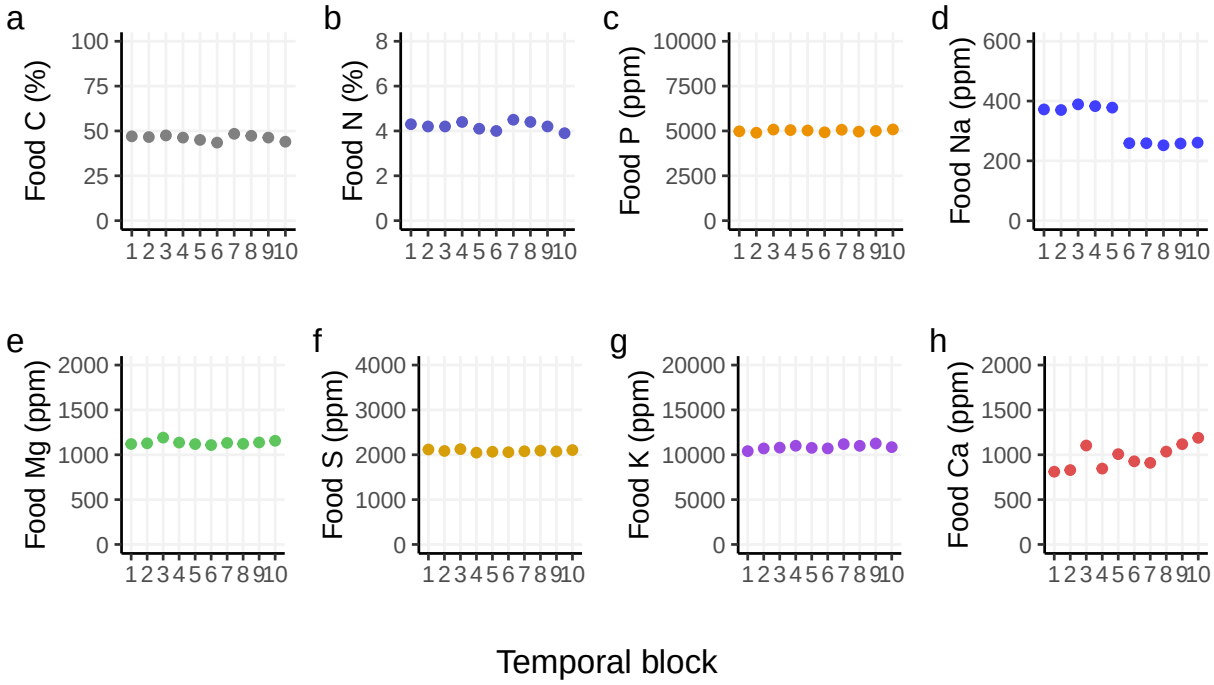

Figure S3. Variation of food chemical composition accross the temporal blocks (years: 2021-2022). Each point represents a composite sample of food representative of the temporal block (three pieces of food per temporal block, one per feeding day). Only Na shows a high variability which might have been caused by a difference. The variation of 100 ppm between the first five blocks and the following can be thought of as adding 0.25 g of NaCl in 4 kg of fresh food, or a difference of 55 µg per day for the larvae of the highest food availability treatment. This variation is less than the one observed in plants grown at constant sodium concentration (G. V. Subbarao and Wheeler, 2003) so it can be considered natural and comparable. The origin of the variation might be due to differences in the molarity of the ampicillin sodium salt solution or in the vitamin mix that we used.

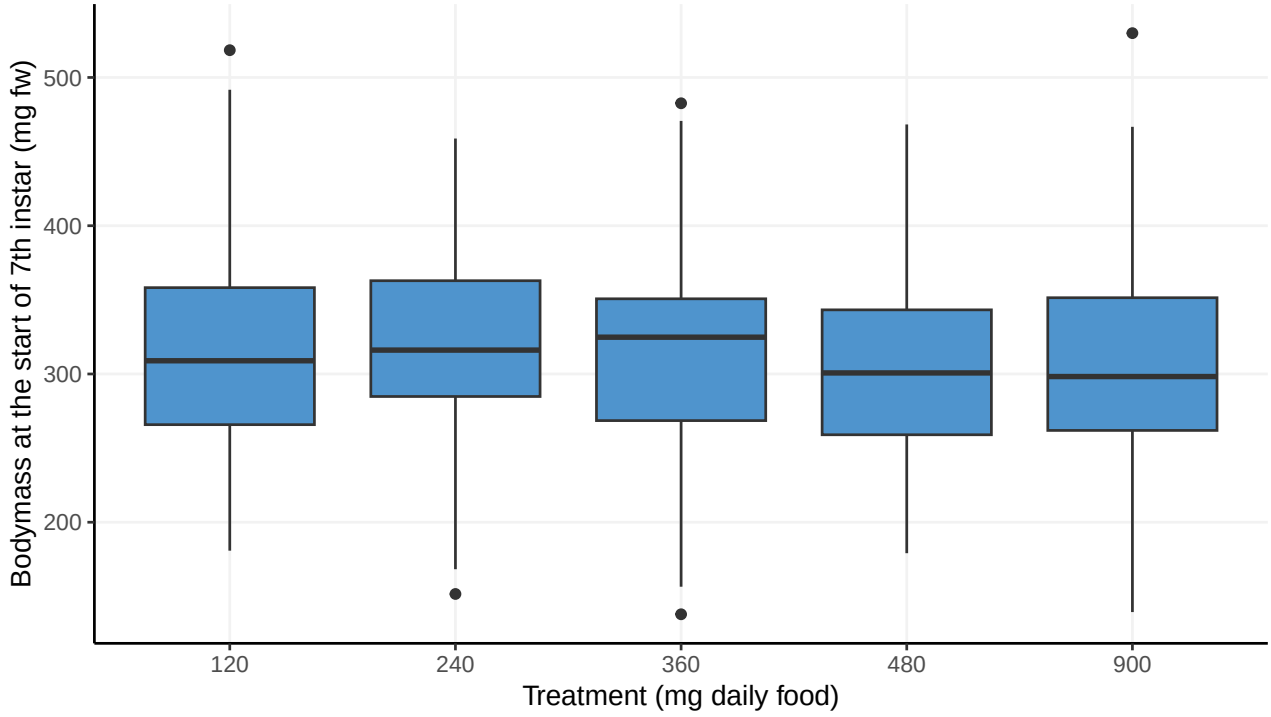

Figure S4. Variation of larvae fresh body mass at the start of the experiment among the five treatments. Each point represents an individual. At the start, larvae are at the very beginning of their seventh larval stage. F-test shows that there was bodymasses did not differ between treatment (p-value = 0.3022).

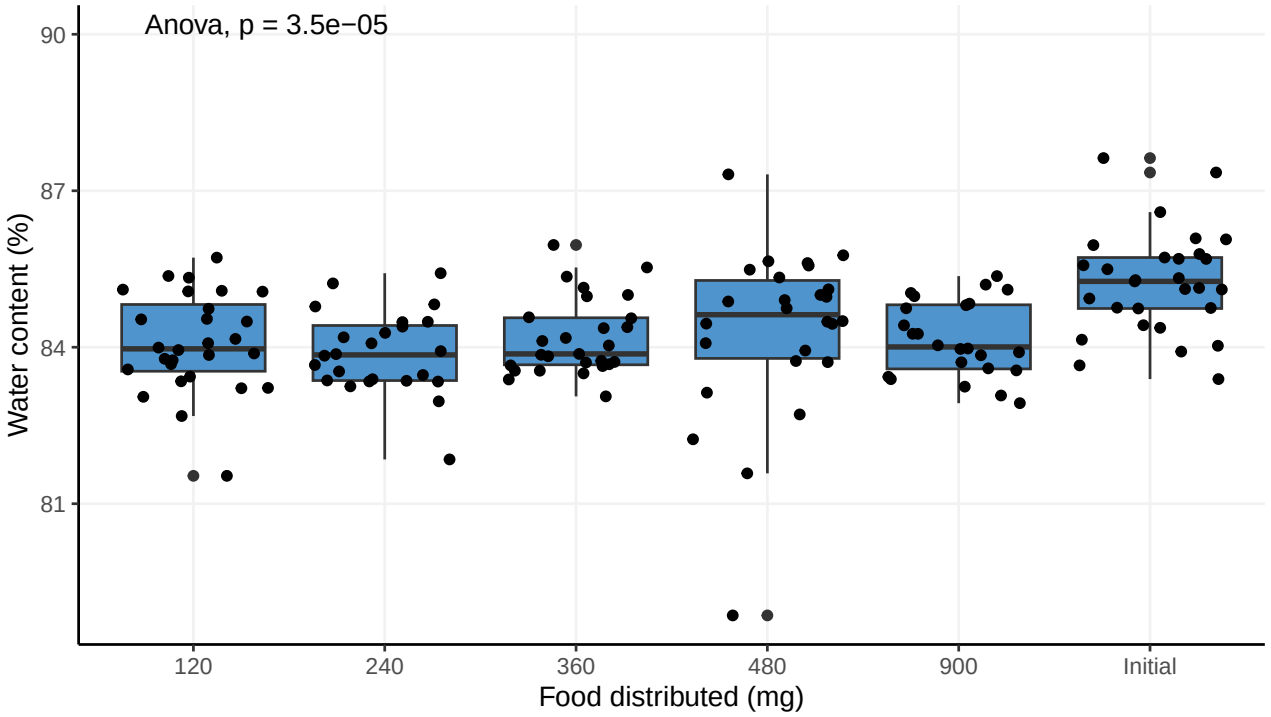

Figure S5. Variation of larvae water content among the five treatments and compared to the initial value. Each point represents an individual. At the start, larvae are at the very beginning of their seventh larval stage. F-test shows that there was bodymasses did not differ between treatment (p-value = 0.3022).

Mass budget

Investigating the total mass budgets mainly consisted of analysing GAMs that were fitted between the various variables of interest and the MSIR. The models were fitted (table S3) and their first derivative was numerically computed to assess the complex effect of MSIR (Figure S6).

O. GAM models

Table S2. Summaries of the four GAMs plotted in fig. 1. MSIR stand for mass-specific intake rate, GR for growth rate, GE for growth efficiency, and AE for assimilation efficiency, edf for effective degrees of freedom. TP refers to thin-plate splines, and AD to adaptive splines. The parameter ϕ for Beta regressions is indicated in parentheses (Wood et al., 2016)

Predictor	Response	n	edf	ref df	n parameters	p	Adjusted R^2	Family	Smoother
MSIR	GR	394	5.2	6.33	10	<2e-16	0.95	Scaled t(6.975,0.023)	TP
MSIR	AE	394	5.04	6.15	10	<2e-16	0.5	Scaled t(5.664,0.038)	TP
MSIR	GE	395	4.98	5.7	10	<2e-16	0.34	Scaled t(5.415,0.021)	AD
GR	GE	394	5.01	5.79	10	<2e-16	0.34	Scaled t(10.03,0.023)	AD

P. Supplementary figures

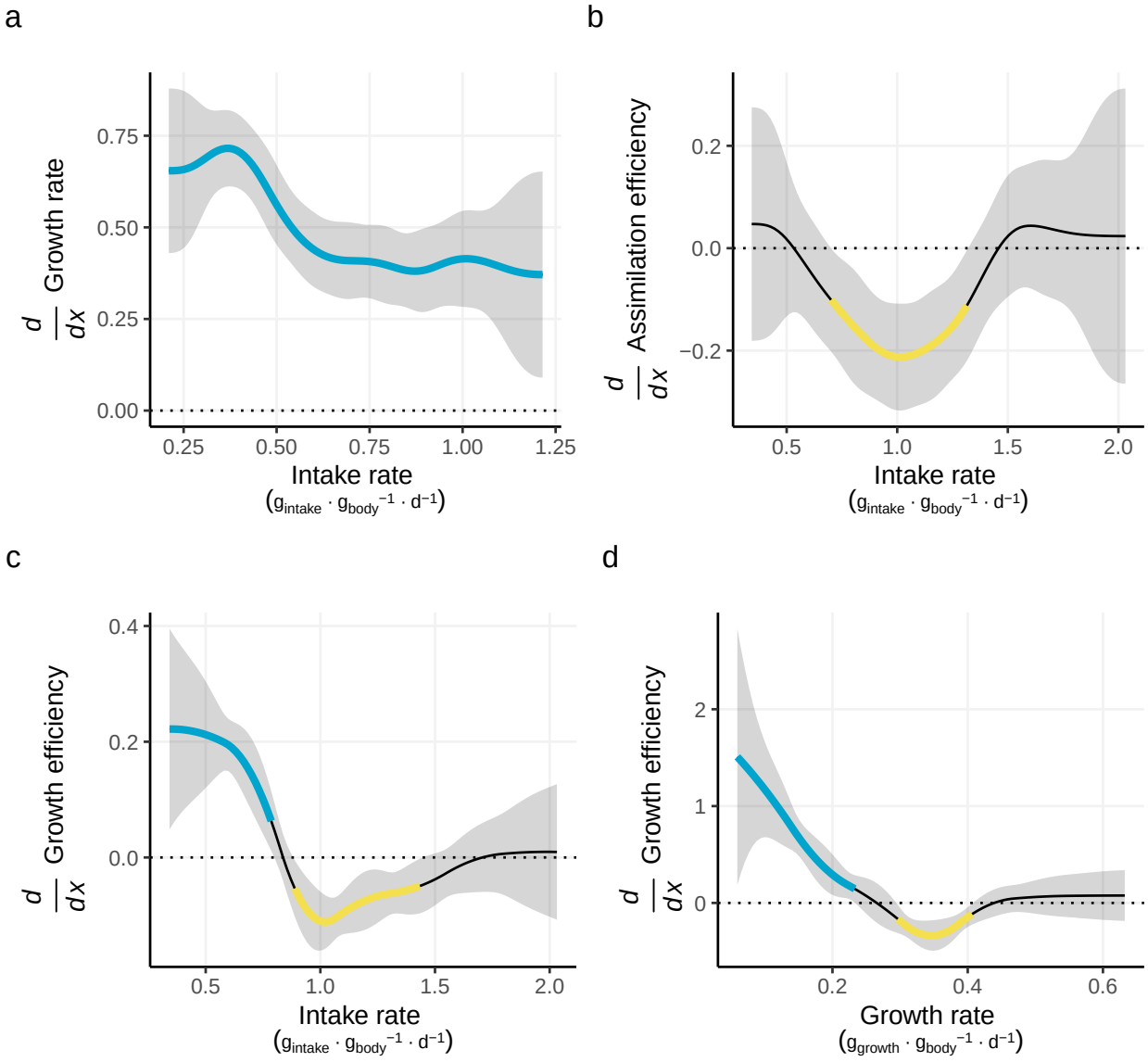

Figure S6. The derivatives, computed as finite differences, of each model plotted in Figure 1. Blue portions of the derivatives highlight domains where the derivative is significantly positive, whereas yellow portions highlight domains where it is negative. Black portions show domains where it is not significantly different from 0. The confidence interval is simultaneous and is computed using the gratia package in R.

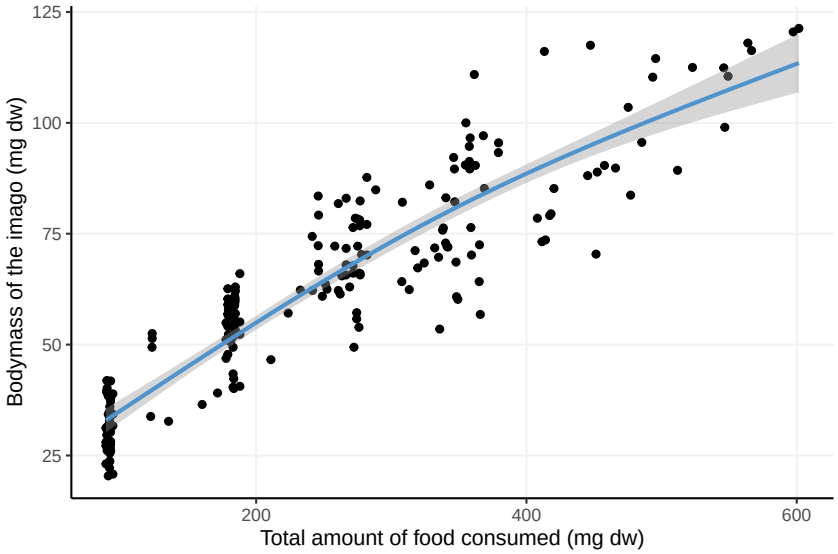

Figure S7. Variation of adult body mass according to food consumed during the experiment. Each point represents an individual.

Nutrients budgets

In this section, we provide further information about the nutrient budget assessment. Individual GAMs for each of the four variables AE, RT, larval and frass nutrient content, all regressed versus MSIR are given in table table S3. We proceed by representing these models in figs. Figure S8, Figure 2, Figure S12, Figure S13. For AE and RT, we also represent their first derivative computed numerically in figs.Figure S9 and Figure S11.

For both AE and RT, a GAM was run with both element and MSIR as dependent variables. Contrasts were estimated for pairs of elements on both the predictions of the model and the trends of the models, allowing to investigate differences between elemental AE (table table S4) and RT (table table S6) and the effect of MSIR thereupon (tables table S5 and table S7 respectively).

Finally, we provide two interesting figures related to the stoichiometric aspects of the experiment, although not intended at first, and specifically about the growth rate hypothesis (Figure S14) and the relationship between stoichiometric stocks in the consumer and its frass (Figure S15)

Table S3. Summaries of element-wise GAM models used to produce the plots in figs. 2, S8, S10, S12 and S13. AE stands for assimilation efficiency, and RT for retention time, edf for effective degrees of freedom. All models were fitted using thin-plate splines and with 10 parameters. The parameter ϕ for Beta regressions is indicated in parentheses (Wood et al., 2016)

Response	Element	n	edf	ref df	p	Adjusted R^2	Family	Link function
Larvae	C	92	1.03	1.06	<2e-16	0.37	gaussian	identity
	N	92	2.42	3.03	<2e-16	0.37		
	P	94	2.8	3.49	<2e-16	0.77		
	Na	94	4.53	5.54	<2e-16	0.71		
	Mg	94	2.74	3.41	5e-03	0.14		
	S	94	4.63	5.65	<2e-16	0.61		
	K	94	3.61	4.45	2.5e-04	0.21		
	Ca	94	3.24	4.01	<2e-16	0.43		
Frass	C	100	1	1	3.1e-05	0.15		
	N	100	1.95	2.44	<2e-16	0.48		
	P	100	5.81	6.96	3.6e-06	0.31		
	Na	98	1.52	1.88	1.2e-03	0.13		
	Mg	100	1.01	1.02	<2e-16	0.41		
	S	100	1.45	1.77	1.4e-03	0.12		
	K	100	4.2	5.15	<2e-16	0.54		
	Ca	100	3.35	4.15	3.8e-04	0.19		
AE	C	100	3.55	4.39	<2e-16	0.66	Beta regression(216.21)	logit
	N	100	4.19	5.14	<2e-16	0.77	Beta regression(188.025)	
	P	100	4.59	5.61	<2e-16	0.66	Beta regression(119.23)	
	Na	98	1	1	<2e-16	0.37	Beta regression(7.454)	
	Mg	100	2.71	3.38	<2e-16	0.61	Beta regression(74.326)	
	S	100	3.45	4.26	<2e-16	0.57	Beta regression(75.659)	
	K	100	4.18	5.13	<2e-16	0.59	Beta regression(76.537)	
	Ca	100	2.48	3.1	<2e-16	0.43	Beta regression(43.478)	
RT	C	92	4.16	5.1	<2e-16	0.96	Gamma	log
	N	92	4.27	5.23	<2e-16	0.95		
	P	94	4.09	5.02	<2e-16	0.94		
	Na	92	2.46	3.07	<2e-16	0.33		
	Mg	94	3.93	4.83	<2e-16	0.88		
	S	94	4.29	5.26	<2e-16	0.97		
	K	94	3.58	4.42	<2e-16	0.74		
	Ca	94	4.04	4.96	<2e-16	0.88		

Q. Absorption efficiencies

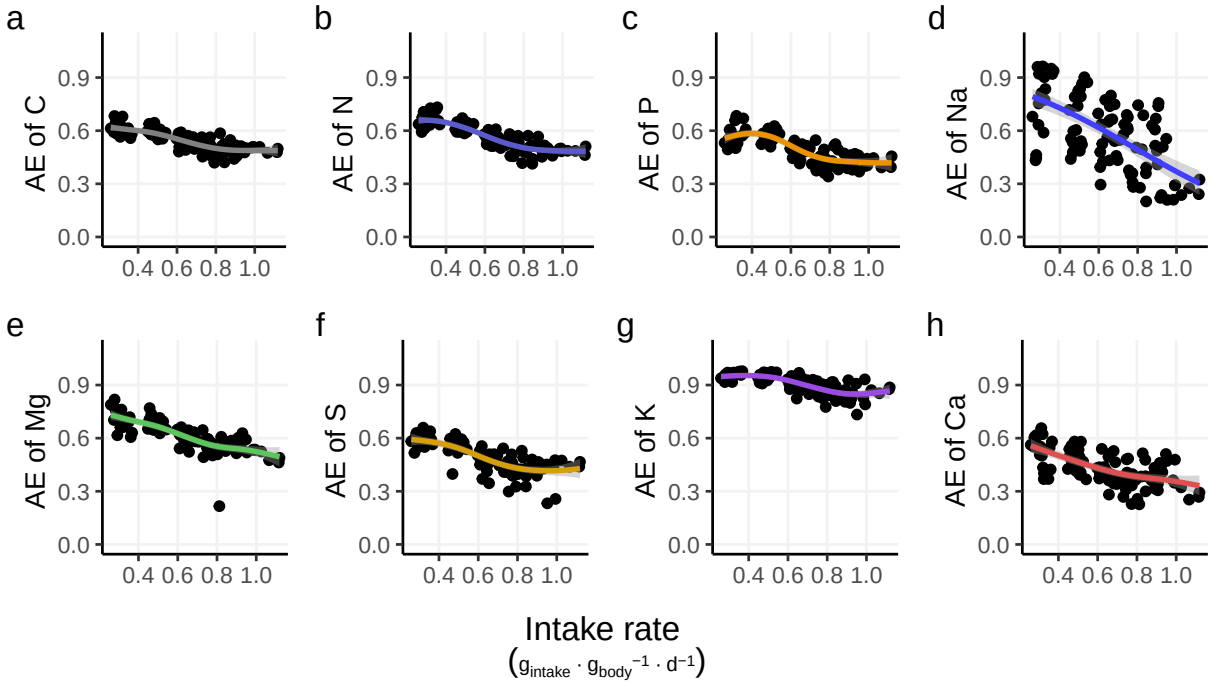

Figure S8. Assimilation efficiencies of the eight tested elements as a function of mass-specific intake rate. Each point is a measurement done on four larvae. Lines are GAMs.

Table S4. Pairwise comparisons of elemental absorption efficiencies predicted by the general GAM model. From left to right: elements being compared, the average difference is their estimate, the standard error associated, the z value for the test followed by the p- and the S- values. Finally, the confidence interval of the difference.

Term	Estimate	Std. Error	z	Pr(>|z|)	S	2.5 %	97.5 %
C - N	-0.0193	0.01150	-1.680	0.09297	3.4	-0.0419	0.00322
C - P	0.0461	0.01156	3.992	**< 0.001**	13.9	0.0235	0.06880
C - S	0.0512	0.01155	4.435	**< 0.001**	16.7	0.0286	0.07388
C - Na	-0.0489	0.01128	-4.340	**< 0.001**	16.1	-0.0710	-0.02684
C - Mg	-0.0695	0.01138	-6.105	**< 0.001**	29.9	-0.0918	-0.04719
C - K	-0.3573	0.00938	-38.080	**< 0.001**	Inf	-0.3757	-0.33893
C - Ca	0.1099	0.01150	9.553	**< 0.001**	69.4	0.0873	0.13240
N - P	0.0655	0.01151	5.688	**< 0.001**	26.2	0.0429	0.08803
N - S	0.0706	0.01150	6.134	**< 0.001**	30.1	0.0480	0.09311
N - Na	-0.0296	0.01123	-2.638	**0.00834**	6.9	-0.0516	-0.00761
N - Mg	-0.0502	0.01133	-4.427	**< 0.001**	16.7	-0.0724	-0.02796
N - K	-0.3380	0.00932	-36.255	**< 0.001**	953.7	-0.3563	-0.31972
N - Ca	0.1292	0.01145	11.282	**< 0.001**	95.6	0.1067	0.15163
P - S	0.0051	0.01156	0.441	0.65927	0.6	-0.0176	0.02775
P - Na	-0.0951	0.01128	-8.427	**< 0.001**	54.7	-0.1172	-0.07297
P - Mg	-0.1156	0.01139	-10.153	**< 0.001**	78.0	-0.1380	-0.09332
P - K	-0.4035	0.00939	-42.966	**< 0.001**	Inf	-0.4219	-0.38506
P - Ca	0.0637	0.01151	5.538	**< 0.001**	25.0	0.0412	0.08627
S - Na	-0.1002	0.01128	-8.883	**< 0.001**	60.4	-0.1223	-0.07808
S - Mg	-0.1207	0.01138	-10.606	**< 0.001**	84.9	-0.1431	-0.09843
S - K	-0.4086	0.00938	-43.539	**< 0.001**	Inf	-0.4270	-0.39017
S - Ca	0.0586	0.01150	5.097	**< 0.001**	21.5	0.0361	0.08117
Na - Mg	-0.0206	0.01110	-1.852	0.06401	4.0	-0.0423	0.00120
Na - K	-0.3084	0.00904	-34.112	**< 0.001**	844.8	-0.3261	-0.29066
Na - Ca	0.1588	0.01122	14.151	**< 0.001**	148.6	0.1368	0.18080
Mg - K	-0.2878	0.00917	-31.371	**< 0.001**	715.2	-0.3058	-0.26983
Mg - Ca	0.1794	0.01133	15.830	**< 0.001**	185.1	0.1572	0.20158
K - Ca	0.4672	0.00932	50.139	**< 0.001**	Inf	0.4489	0.48545

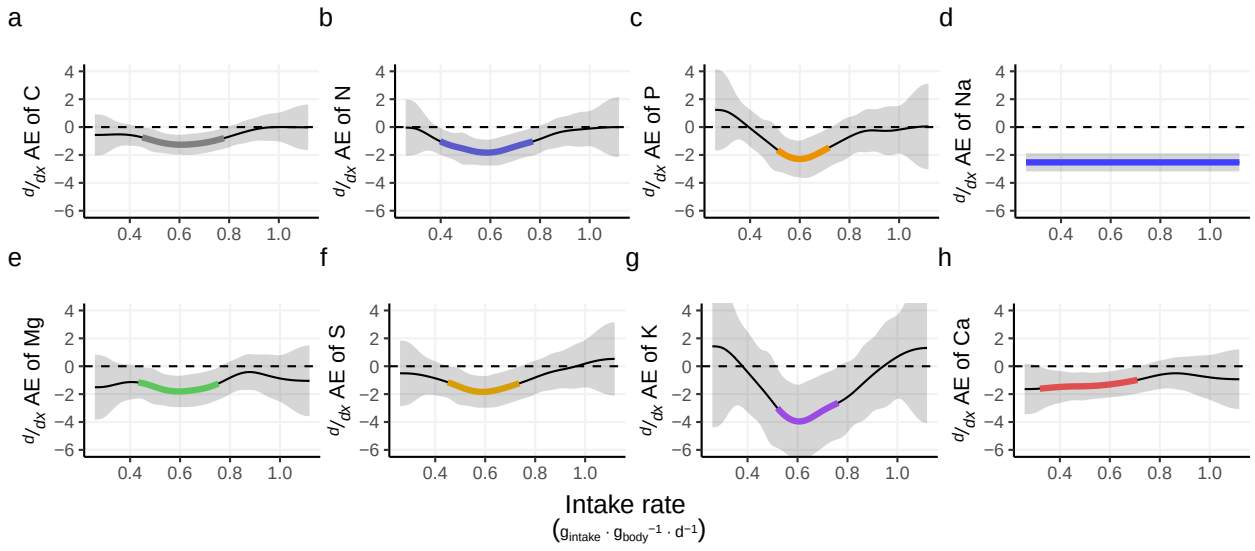

Figure S9. First derivatives of assimilation efficiencies of the eight tested elements as a function of mass-specific intake rate, estimated through finite difference quotient. The confidence interval is of the simultaneous type, coloured are the intervals over which the derivative is significantly different from 0.

Table S5. Pairwise comparisons of the effect of intake rate on elemental absorption efficiencies predicted by the general GAM model. From left to right: elements being compared, the average difference in the slopes (see fig S9), the standard error associated, the z value for the test followed by the p- and the S- values. Finally, the confidence interval of the difference.

Term	Estimate	Std. Error	z	Pr(>|z|)	S	2.5 %	97.5 %
C - Ca	0.04593	0.0315	1.457	0.14520	2.8	-0.015868	0.1077
C - K	-0.03652	0.0260	-1.406	0.15960	2.6	-0.087410	0.0144
C - Mg	0.05767	0.0297	1.940	0.05239	4.3	-0.000596	0.1159
C - N	0.04256	0.0304	1.401	0.16118	2.6	-0.016977	0.1021
C - Na	0.26265	0.0280	9.385	**< 0.001**	67.1	0.207801	0.3175
C - P	0.00797	0.0345	0.231	0.81745	0.3	-0.059704	0.0756
C - S	0.03066	0.0325	0.944	0.34534	1.5	-0.033016	0.0943
Ca - K	-0.08245	0.0276	-2.988	**0.00280**	8.5	-0.136525	-0.0284
Ca - Mg	0.01174	0.0312	0.377	0.70626	0.5	-0.049328	0.0728
Ca - N	-0.00337	0.0318	-0.106	0.91559	0.1	-0.065652	0.0589
Ca - Na	0.21672	0.0295	7.347	**< 0.001**	42.2	0.158904	0.2745
Ca - P	-0.03796	0.0358	-1.061	0.28853	1.8	-0.108062	0.0321
Ca - S	-0.01527	0.0338	-0.452	0.65133	0.6	-0.081520	0.0510
K - Mg	0.09419	0.0255	3.692	**< 0.001**	12.1	0.044187	0.1442
K - N	0.07908	0.0263	3.011	**0.00261**	8.6	0.027602	0.1306
K - Na	0.29917	0.0235	12.754	**< 0.001**	121.3	0.253195	0.3451
K - P	0.04449	0.0310	1.436	0.15089	2.7	-0.016216	0.1052
K - S	0.06717	0.0287	2.342	**0.01916**	5.7	0.010967	0.1234
Mg - N	-0.01511	0.0300	-0.504	0.61438	0.7	-0.073896	0.0437
Mg - Na	0.20498	0.0276	7.436	**< 0.001**	43.1	0.150948	0.2590
Mg - P	-0.04970	0.0342	-1.454	0.14601	2.8	-0.116715	0.0173
Mg - S	-0.02702	0.0321	-0.841	0.40036	1.3	-0.089985	0.0359
N - Na	0.22009	0.0283	7.787	**< 0.001**	47.0	0.164693	0.2755
N - P	-0.03459	0.0348	-0.995	0.31957	1.6	-0.102711	0.0335
N - S	-0.01191	0.0327	-0.364	0.71599	0.5	-0.076049	0.0522
Na - P	-0.25468	0.0327	-7.792	**< 0.001**	47.1	-0.318740	-0.1906
Na - S	-0.23200	0.0305	-7.602	**< 0.001**	45.0	-0.291810	-0.1722
P - S	0.02269	0.0366	0.620	0.53549	0.9	-0.049071	0.0944

R. Retention times

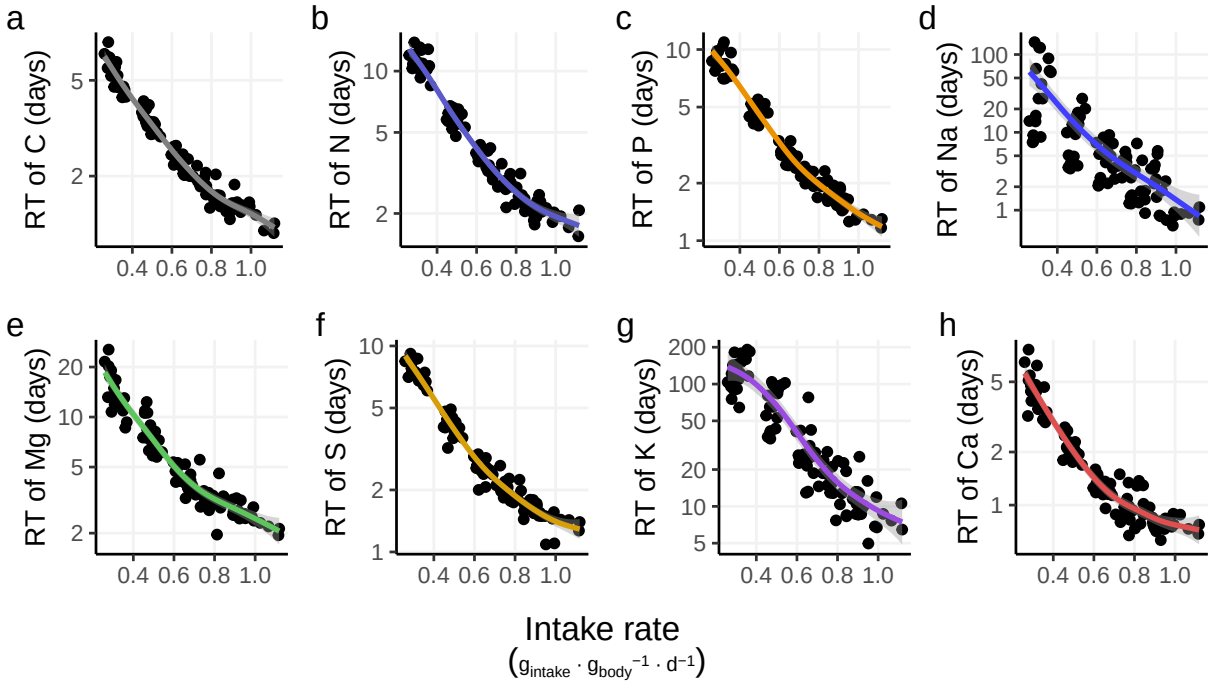

Figure S10. Retention times of the eight tested elements as a function of mass-specific intake rate. Each point is a measurement done on four larvae. Lines are GAMs.

Table S6. Pairwise comparisons of elemental retention times predicted by the general GAM model. From left to right: elements being compared, the average difference is their estimate, the standard error associated, the z value for the test followed by the p- and the S- values. Finally, the confidence interval of the difference.

Term	Estimate	Std. Error	z	Pr(>|z|)	S	2.5 %	97.5 %
C - N	-2.191	0.212	-10.35	**<0.001**	81.0	-2.6062	-1.777
C - P	-1.046	0.174	-6.01	**<0.001**	29.0	-1.3876	-0.705
C - S	-0.655	0.161	-4.06	**<0.001**	14.3	-0.9720	-0.339
C - Na	-9.995	0.708	-14.13	**<0.001**	148.1	-11.3822	-8.608
C - Mg	-3.682	0.264	-13.95	**<0.001**	144.4	-4.1996	-3.165
C - K	-47.632	2.033	-23.43	**<0.001**	400.8	-51.6170	-43.647
C - Ca	0.943	0.123	7.68	**<0.001**	45.8	0.7022	1.183
N - P	1.145	0.235	4.87	**<0.001**	19.7	0.6837	1.606
N - S	1.536	0.226	6.79	**<0.001**	36.4	1.0926	1.979
N - Na	-7.804	0.725	-10.76	**<0.001**	87.3	-9.2252	-6.383
N - Mg	-1.491	0.308	-4.84	**<0.001**	19.6	-2.0942	-0.887
N - K	-45.441	2.039	-22.28	**<0.001**	363.0	-49.4377	-41.444
N - Ca	3.134	0.200	15.64	**<0.001**	180.8	2.7414	3.527
P - S	0.391	0.191	2.04	**0.0412**	4.6	0.0156	0.766
P - Na	-8.949	0.715	-12.52	**<0.001**	117.0	-10.3505	-7.548
P - Mg	-2.636	0.283	-9.30	**<0.001**	66.0	-3.1912	-2.080
P - K	-46.586	2.036	-22.88	**<0.001**	382.6	-50.5758	-42.596
P - Ca	1.989	0.160	12.42	**<0.001**	115.2	1.6752	2.303
S - Na	-9.340	0.712	-13.12	**<0.001**	128.1	-10.7355	-7.944
S - Mg	-3.027	0.276	-10.97	**<0.001**	90.7	-3.5672	-2.486
S - K	-46.977	2.035	-23.09	**<0.001**	389.4	-50.9646	-42.989
S - Ca	1.598	0.146	10.92	**<0.001**	89.8	1.3114	1.885
Na - Mg	6.313	0.742	8.51	**<0.001**	55.6	4.8588	7.768
Na - K	-37.637	2.148	-17.52	**<0.001**	225.9	-41.8471	-33.426
Na - Ca	10.938	0.704	15.53	**<0.001**	178.3	9.5578	12.319
Mg - K	-43.950	2.045	-21.49	**<0.001**	337.8	-47.9589	-39.941
Mg - Ca	4.625	0.255	18.13	**<0.001**	241.7	4.1250	5.125
K - Ca	48.575	2.032	23.90	**<0.001**	417.1	44.5922	52.558

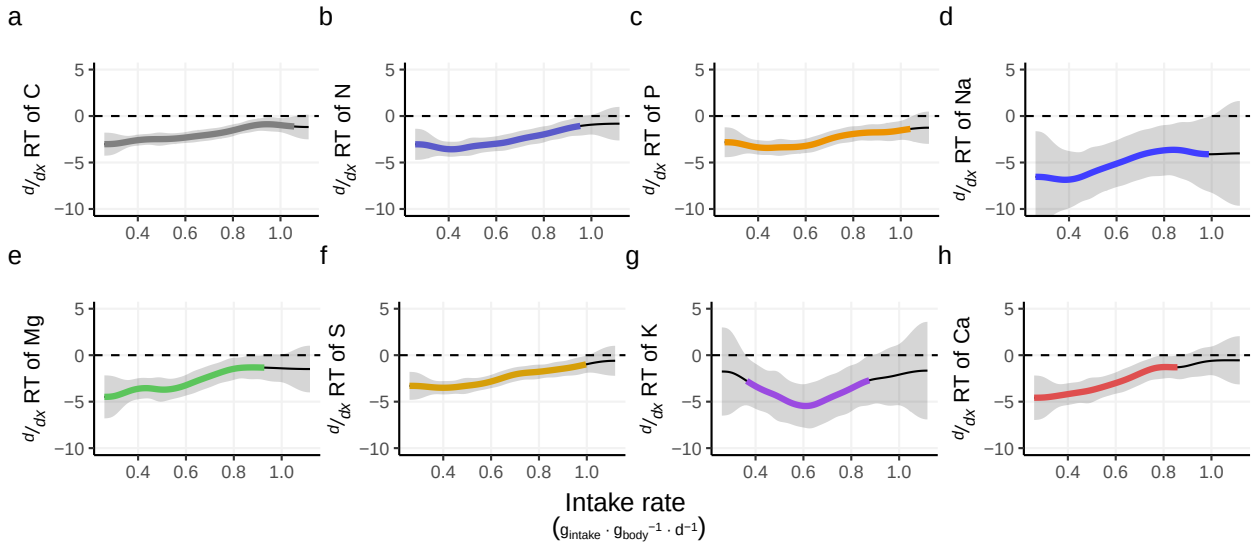

Figure S11. First derivatives of retention time of each element as a function of mass-specific intake rate, estimated through finite difference quotient. The confidence interval is of the simultaneous type, coloured are the intervals over which the derivative is significantly different from 0.

Table S7. Pairwise comparisons of the effect of intake rate on elemental retention times predicted by the general GAM model. From left to right: elements being compared, the average difference in the slopes (see fig S11), the standard error associated, the z value for the test followed by the p- and the S- values. Finally, the confidence interval of the difference.

Term	Estimate	Std. Error	z	Pr(>|z|)	S	2.5 %	97.5 %
C - Ca	0.0636	0.700	0.0908	0.92762	0.1	-1.309	1.436
C - K	81.9584	15.847	5.1719	**< 0.001**	22.0	50.899	113.017
C - Mg	9.1689	1.676	5.4700	**< 0.001**	24.4	5.884	12.454
C - N	5.0965	1.187	4.2931	**< 0.001**	15.8	2.770	7.423
C - Na	-60.3468	9.324	-6.4721	**< 0.001**	33.3	-78.622	-42.072
C - P	3.0777	0.910	3.3826	**< 0.001**	10.4	1.294	4.861
C - S	2.2309	0.873	2.5558	**0.01060**	6.6	0.520	3.942
Ca - K	81.8948	15.848	5.1674	**< 0.001**	22.0	50.832	112.957
Ca - Mg	9.1053	1.692	5.3811	**< 0.001**	23.7	5.789	12.422
Ca - N	5.0329	1.209	4.1613	**< 0.001**	14.9	2.662	7.403
Ca - Na	-60.4104	9.327	-6.4769	**< 0.001**	33.3	-78.691	-42.130
Ca - P	3.0141	0.939	3.2107	**0.00132**	9.6	1.174	4.854
Ca - S	2.1672	0.903	2.4002	**0.01639**	5.9	0.397	3.937
K - Mg	-72.7895	15.921	-4.5718	**< 0.001**	17.7	-103.995	-41.584
K - N	-76.8619	15.877	-4.8410	**< 0.001**	19.6	-107.981	-45.743
K - Na	-142.3052	18.375	-7.7447	**< 0.001**	46.6	-178.319	-106.292
K - P	-78.8807	15.859	-4.9738	**< 0.001**	20.5	-109.964	-47.797
K - S	-79.7275	15.857	-5.0279	**< 0.001**	20.9	-110.807	-48.648
Mg - N	-4.0724	1.945	-2.0941	**0.03625**	4.8	-7.884	-0.261
Mg - Na	-69.5157	9.451	-7.3557	**< 0.001**	42.3	-88.038	-50.993
Mg - P	-6.0912	1.789	-3.4049	**< 0.001**	10.6	-9.597	-2.585
Mg - S	-6.9380	1.770	-3.9188	**< 0.001**	13.5	-10.408	-3.468
N - Na	-65.4433	9.376	-6.9798	**< 0.001**	38.3	-83.820	-47.066
N - P	-2.0188	1.342	-1.5047	0.13240	2.9	-4.648	0.611
N - S	-2.8656	1.317	-2.1762	**0.02954**	5.1	-5.447	-0.285
Na - P	63.4245	9.345	6.7869	**< 0.001**	36.3	45.108	81.741
Na - S	62.5776	9.342	6.6988	**< 0.001**	35.5	44.269	80.887
P - S	-0.8469	1.074	-0.7888	0.43022	1.2	-2.951	1.257

S. Frass and larvae

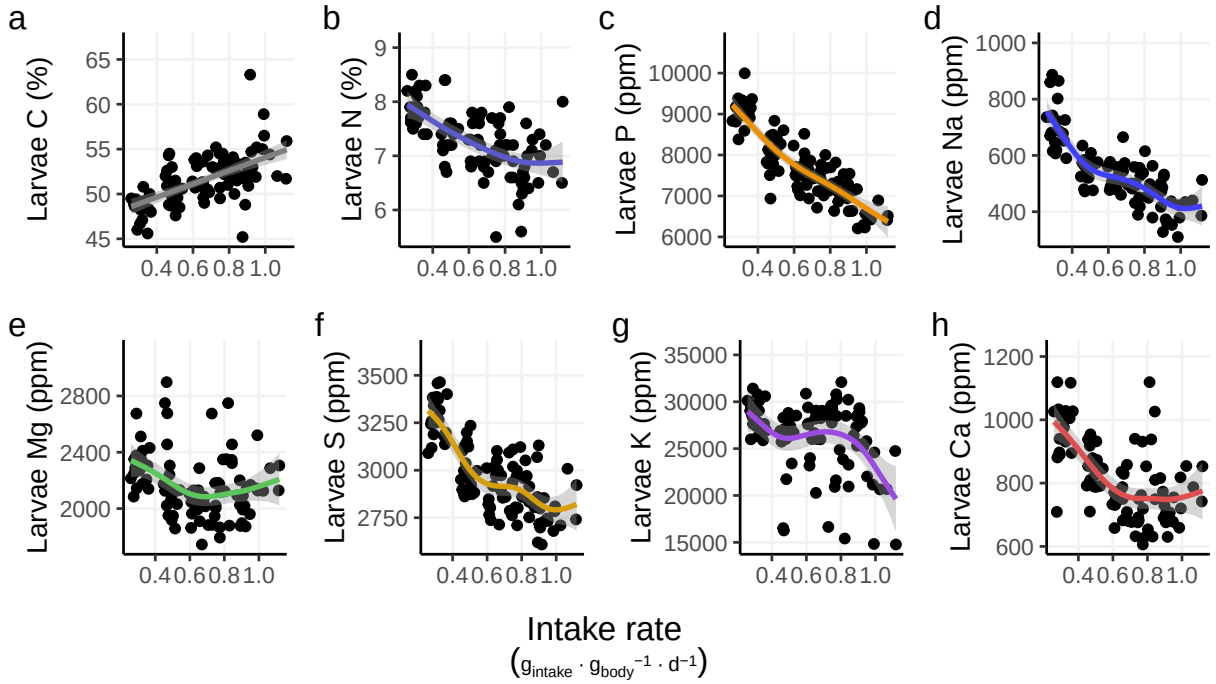

Figure S12. Body content in the eight tested elements as a function of mass-specific intake rate. Each point is a measurement done on four larvae. Lines are GAMs.

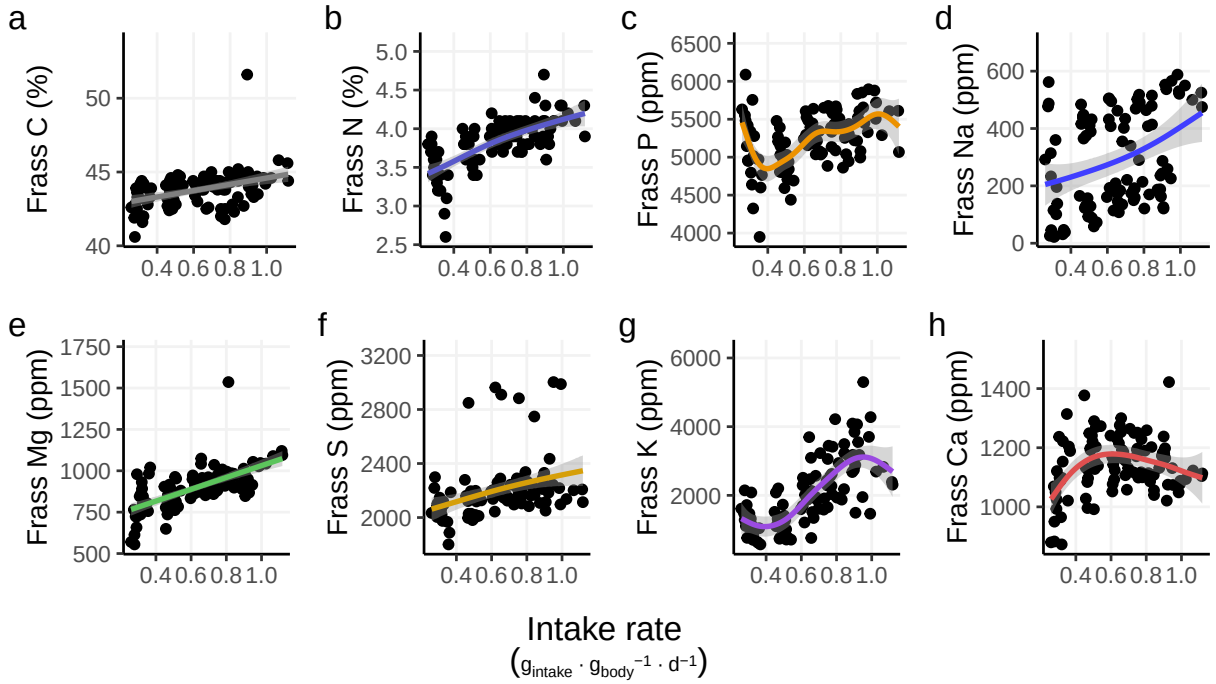

Figure S13. Frass (egestion) content in the eight tested elements according to the mass-specific intake rate. Each point is a measurement done on four larvae. Lines are GAMs

T. Stoichiometry

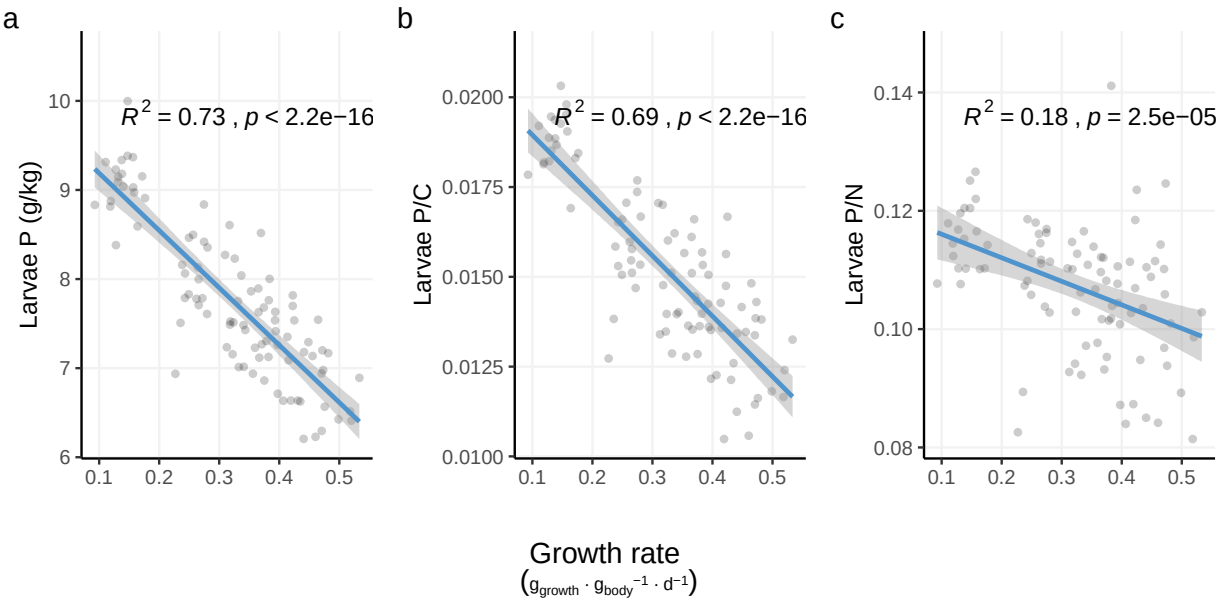

Figure S14. Relationship between larval P, P/C and P/N and growth rate. Each point represents a group of four larvae. The regression line is a linear model, of which R^2 and Pearson correlation p-values are shown.

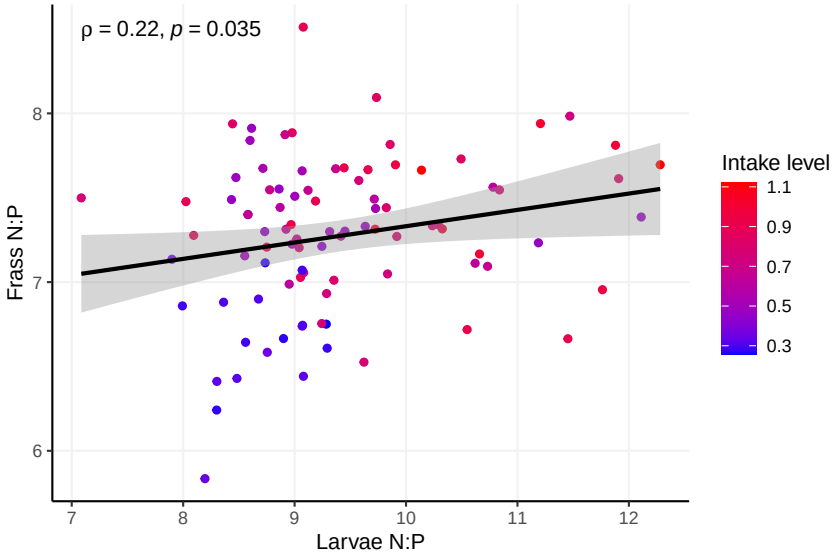

Figure S15. Relationship between larvae and frass N/P. Each point represents a group of four larvae. The regression line represents a cubic spline. In colour is shown intake level measured as mass-specific intake rate (mg $\times$ mg $^{-1}$ $\times$ day $^{-1}$ in fresh weight).

U. Note on the growth rate hypothesis

Although our experiment was not designed to test the growth rate hypothesis (GRH) – which states fast-growing organisms are high in P (Sterner and Hessen, 1994; Isanta-Navarro et al., 2022)–, our data allows us to assess the relevance of the theory in the context of a gradient of food availability. Opposite to the GRH, we observed a decrease in body P, P/N or P/C content with growth rate (Figure S14). This indicates that in our experiment, faster-growing animals were poorer in P than slower-growing ones and had a stronger decrease in P than in N content with growth rate (Figure 3c). Many experiments confirming this hypothesis at the intraspecific level forced the differences in growth by manipulating the P contents of food (Elser et al., 2003, 2006; Kyle et al., 2006). Conversely, we show here that under constant food stoichiometry, a lower growth rate during food restriction does not necessarily imply lower body P and body N/P increase. In our experiment, high intake rates allowed the building of a lot of C-rich lipidic reserves, therefore increasing C-nutrient ratios at high growth rates and diluting P content. At low intake, biosynthesis

likely focused on building N-rich proteins to maintain functioning. Variation in lipid storage combined with the absence of P limitation ultimately may have masked the predictions expected under the growth rate hypothesis.

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