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Diet Mixing: Do Animals Integrate Growth or Resources across Temporal Heterogeneity?

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abstract: Animals commonly experience spatial and temporal variation in resource quality, thus experiencing temporally variable diets. Methods for scaling up growth in component patches to long-term growth across heterogeneity are seldom explicitly considered. Long-term growth is sometimes considered to be a weighted average of growth rates on component diets (growth integration). However, if animals integrate resources across high- and low-quality diets, their long-term growth may be greater than predicted from diet-specific growth rates (resource integration). We measured biomass growth rates of seven *Daphnia* species exposed to different types of diel variation in algal phosphorus (P) content. Support for resource integration was found for four of the seven species, which achieved near maximal growth when high-P food was available for at least 12 h. In contrast, no support for resource integration was found for the other three species. These three species achieved only one-half maximal growth rate under the same conditions and could be considered growth integrators. The type of integration could be predicted from the degree of stoichiometric homeostasis. Species with weak homeostatic regulation exhibited a capacity for resource integration. Resource integrators should have an advantage in heterogeneous environments.

Keywords: ecological stoichiometry, homeostasis, *Daphnia*, phosphorus limitation, phosphorus storage, temporal diet mixing.

Introduction

Animals experience spatial and temporal variation in resource quality, which influences multiple aspects of their ecology, including movement (Jones et al. 2006), competition (Chesson 2000), and fitness (DeMott et al. 2004). To succeed in nutritionally complex environments, animals must locate and acquire nutrients while balancing their nutritional demands against other biotic and abiotic factors, such as predation or temperature. When they are able to move without restrictions among habitats or diets, animals can be remarkably adept at mixing diets to optimize the intake of multiple nutrients (Behmer 2009). But biotic and abiotic factors often preclude intake of the optimal mixture (e.g., Power et al. 1989; Scrimgeour and Culp 1994; Lewis 2001; Bakker et al. 2005; Maclean et al. 2005; Hansson and Hylander 2009). When choices are restricted, strategies for integrating across heterogeneity may play key roles in ecological success and evolutionary fitness. In these situations, the long-term fitness of an individual is related to patch-specific fitness; however, the nature of integration across patches has seldom been explicitly considered.

Two approaches have been used to specify the relationships between long-term fitness and patterns of patch use. The most parsimonious approach is to experimentally identify how critical abiotic and biotic factors influence patch choice and shape long-term fitness (e.g., Power et al. 1989). This approach estimates long-term fitness within complex landscapes; however, it can be very labor intensive and case specific. It does not reliably extrapolate to novel landscapes because the relationship between patch use and fitness is not explicitly determined. The more common alternative is to identify the abiotic and biotic determinants of patch quality (Iversen 1974; Sterner 1993; Vos et al. 2002) and use the relationship between patch quality and fitness to predict long-term fitness in novel heterogeneous environments, scaling up from knowledge of individual patches to predict success in a complex environment. This inductive approach is built on a mechanistic consideration of the characteristics of quality; however, when scaling component results to heterogeneous environments, diet-specific growth rates and patch use frequency must be combined to estimate long-term growth.

When animals cannot store resources from high-quality patches and use them in low-quality patches, long-term growth may be a simple linear weighting of growth in individual patches (proportion of time in each patch times growth rate in that patch, summed over patches). Such animals are described here as growth integrators because they integrate growth across patches. However, patch qual-

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ity is often determined by nutrients such as protein, carbohydrates, or phosphorus that animals may store and transport among patches. When excess resources are stored in one patch and subsequently used to supplement growth in low-quality patches, long-term fitness is likely to be greater than predicted by simple linear weighting of growth across patches. These animals are termed here resource integrators. Growth integration is most easily scalable theoretically across different types of variation, but the preponderance of storage molecules among animals (Woods et al. 2002; Lee et al. 2006; Raubenheimer and Jones 2006) indicates that temporal resource mixing may often influence long-term fitness. A means to understand and predict these two different types of population dynamics is needed.

To determine how temporal diet mixing affects long-term growth, it is necessary to explicitly track the availability and incorporation of limiting resources. Ecological stoichiometry (Sterner and Elser 2002) uses a mass balance and elemental ratios to determine how a stoichiometrically imbalanced diet influences fitness and food web dynamics. A critical parameter in ecological stoichiometry is the degree of elemental regulation, or homeostasis. Variation in stoichiometric homeostasis reflects the degree of elemental depletion during nutrient limitation as well as a species' capacity for elemental storage during periods of excess. Few stoichiometric studies have examined spatial or temporal heterogeneity. Sterner and Schwalbach (2001) examined how temporal mixing of high- and low-phosphorus (P) diets influenced the growth rate of *Daphnia magna*. They showed that what we call here growth integration underestimates long-term dynamics on temporally mixed diets, presumably because *D. magna* temporally mixes P across diets.

Members of the genus *Daphnia* often play a keystone role in lakes (Elser et al. 1988; Rudstam et al. 1993) and are an excellent model species for this type of study. They are generalist feeders that commonly experience both temporal and spatial variation in food quality, which is determined by a number of factors, including food particle size, toxicity, essential fatty acids, and P content (Sterner and Schulz 1998). "Seston" refers to the collection of particles suspended in lake waters. The seston phosphorus to carbon (P : C) ratio is one determinant of food quality for *Daphnia* (Sterner 1993; DeMott and Pape 2005), which actively identify and congregate within patches having high food P : C ratios (Schatz and McCauley 2007). Seston P : C is both spatially and temporally heterogeneous (Sterner et al. 1997; Hessen et al. 2005; Berger et al. 2006), varying seasonally as well as over time spans of hours to days (Cunningham and Maas 1978; Dickman et al. 2006). Seston P : C varies in response to gradients of nutrient mixing (Hall et al. 2005), light (Sterner et al. 1997), and grazing (Tessier et al. 2001). During diurnal migrations, vertically migrating zooplankton often consume P-rich algae in cold, deep waters during daytime hours and P-poor food in warm, shallow waters at night (DeMott et al. 2004). The wealth of information available on P stoichiometry and homeostasis for members of this genus makes *Daphnia* an ideal model group.

Given the many potential complexities of spatial and temporal heterogeneity of food quality in natural environments and the unknown nature of biotic response to this heterogeneity, it might seem difficult, if not impossible, to define a framework to scale up from the patch to the landscape scale. In this article, we suggest that scaling of growth from individual patches to long-term dynamics in complex landscapes may be achievable, using simple principles of stoichiometric homeostasis. We first evaluate this hypothesis with two stoichiometrically explicit models of population growth. Then, because *Daphnia* species have different degrees of stoichiometric homeostasis (DeMott and Pape 2005), we test this hypothesis using a comparative framework. *Daphnia* are a well-suited model organism for this study because juvenile body mass growth rates, which can be measured in short-term (<1 week) experiments, are closely related to population growth rates. The relationship between juvenile growth rates and population growth rates holds across species, within a species by genotype, and across feeding treatments (Lampert and Trubetskova 1996; Ferrão Filho et al. 2005). Specifically, we use seven *Daphnia* species to ask whether the ability to temporally mix resources across diets is linked to their stoichiometric homeostasis.

Theoretical Expectations

We argue that the two integration strategies described here are fundamentally linked to the degree of stoichiometric homeostasis exhibited by a species. If a species strictly balances nutrient homeostasis through intake regulation or assimilation, instantaneous growth will vary instantaneously with food quality (fig. 1*a*). When this response is summed over multiple periods of variability, long-term growth will be the temporally weighted average of diet-specific growth rates. Thus, it is growth that is integrated across patches. This strategy produces a positive linear relationship between growth (μ) and the proportion of time spent in high-quality food (F; fig. 1*b*). Note that these species grow slower over the long term than they would on a mixed diet of similar mean quality (fig. 1*b*). Thus, an attempt to measure overall habitat quality by a spatially or temporally weighted sum of within-patch qualities would produce an incorrect picture.

In contrast, a weakly homeostatic species can utilize resources obtained in rich patches to supplement growth

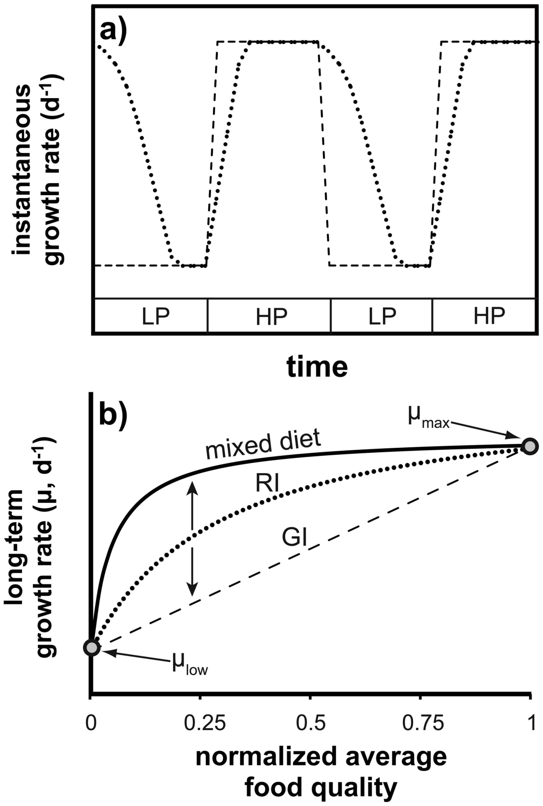

Figure 1: Schematic showing the short-term (*a*) and long-term (*b*) responses of growth integrators (GIs) and resource integrators (RIs) to heterogeneity in diet phosphorus : carbon (P : C) ratio. *a*, Instantaneous growth rate as a function of time for an animal temporally mixing low-phosphorus (LP) and high-phosphorus (HP) algae. Two potential responses exist. Growth could immediately respond to diet quality, producing synchrony between growth and diet, resulting in the square function (*dashed line*). Alternatively, asynchrony between growth and diet results when P is mixed across diets (*dotted line*). *b*, Long-term growth rate for animals consuming a diet that either switches, with variable frequency, between LP and HP algae (*dashed and dotted lines*) or is a mixture of LP and HP algae (*solid line*). Mean daily food quality was normalized by the P content of the diet and ranges from 100% LP algae (0) to 100% HP algae (1). Under constant food supply, a saturating relationship exists between long-term growth rate and mean food quality (*solid line*). When food supply varies, long-term growth rate could respond to mean food quality following two potential classes of relationships. The dashed line (GI) in *b* is the long-term result of growth described by the square function in *a*, whereas the dotted line (RI) corresponds to the curvilinear line (*dotted line*) in *a*. The nonlinear relationship exhibited by RI varies between the GI response (i.e., no resource integration) and the mixed-diet curve as a function of how efficiently excess P is mixed across diets.

in poor patches; in such cases, shifts in instantaneous growth will lag behind shifts in food quality (fig. 1*a*). Specifically, as a resource integrator moves from a rich to a poor patch, stored nutrients may be used to maintain rapid growth. Following the transition to the low-quality patch, growth slowly declines through time, as stored resources are incorporated into new growth and eventually exhausted. The shape and duration of the decline in growth rate depend on the relative magnitude of nutrient stores as well as how rapidly stores are utilized. When summed over days, the long-term growth of a resource integrator produces a curvilinear, saturating relationship between μ and F (fig. 1*b*). The most effective resource integrators would transfer all ingested resources in excess of the requirements of maximum growth from the rich patch to the poor patch. For these species, the nonlinear relationship should approach that seen between long-term growth rate and a mixed diet with the same mean resource level (fig. 1*b*). Thus, there is in theory a gradient of ability to integrate resources, beginning with species incapable of integrating any resources—a condition termed growth integration—and ending with very efficient resource integrators, species integrating all of a resource across diets. Hypothetically, a species' capacity for resource integration is determined by its degree of stoichiometric homeostasis.

To explore the mechanisms linking P balance and the type of integration, we first constructed and analyzed a population growth model for a homeostatic and plastic grazer. We then measured the resource integrative ability of seven *Daphnia* species, exploring relationships among stoichiometric homeostasis and growth patterns in habitats with variation in nutritional quality.

Methods

Population Growth Models

We used a suite of models to examine the influence of P homeostasis on the short- and long-term patterns of population growth in habitats with heterogeneous resource quality. We start with a base model (homeostatic), similar to other stoichiometrically explicit models (Hall 2004; Loladze et al. 2000), in that the grazer instantaneously uses ingested nutrients for new biomass with a fixed stoichiometric ratio. The next model (plastic), an extension of a model presented by Grover (2003), allows for variable grazer stoichiometry. Parameters for both models are listed in table A1 in the online edition of the *American Naturalist*.

Because our focus is on animal production dynamics, the models do not simulate algal dynamics; algal densities (A) and carbon biomass ($Q_{A,\mathrm{C}}$) are maintained at constant levels. Variation in resource quality was imposed by varying algal P content ($Q_{A,\mathrm{P}}$) in a square wave fashion between $Q_{A,\mathrm{P\text{-}LP}}$ and $Q_{A,\mathrm{P\text{-}HP}}$ (LP, low phosphorus; HP, high phosphorus) as a function of time based on the parameter S, the proportion of each day the grazer consumes high-quality algae ($Q_{A,\mathrm{P\text{-}HP}}$).

Homeostatic Model. The homeostatic model describes the population dynamics of a grazer with a fixed P : C stoichiometry of growth:

$$\frac{dZ}{dt} = \mu_{\mathrm{diet}}Z - mZ, \tag{1}$$

where Z is the zooplankton density (individual L^{-1}), μ_{diet} is the grazer's reproductive rate (day^{-1}) for a given diet of either HP or LP algae, and m is mortality rate (day^{-1}).

Plastic Model. The plastic model, based on Grover (2003), uses two differential equations to describe the dynamics of a grazer population with a variable P : C stoichiometry. The first is the equation for zooplankton dynamics:

$$\frac{dZ}{dt} = \mu Z - mZ, \tag{2}$$

where μ is the reproductive rate (day^{-1}) of the grazer population. Reproductive rate (μ) is dependent on the grazer's stores of limiting nutrients:

$$\mu = \mu_{\max}\left[1 - \max_i\left(\frac{Q_{Z,i}^{\max} - Q_{Z,i}}{Q_{Z,i}^{\max} - Q_{Z,i}^{\min}}\right)\right], \tag{3}$$

where $\mu_{\max}$ is the maximum reproductive rate of the grazer (day^{-1}), i is C or P, $Q_{Z,i}$ is the body elemental content or quota of the grazer (mol nutrient $\mathrm{individual}^{-1}$), and $Q_{Z,i}^{\min}$ and $Q_{Z,i}^{\max}$ are the minimum and maximum grazer elemental contents, respectively. DeMott et al. (1998) describes a similar positive linear relationship between growth and body P for P-limited *Daphnia*. The model assumes a similar relationship for C as for P, though potential variation in $Q_{Z,\mathrm{C}}$ is tightly constrained and therefore has a limited influence on dynamics (table A1). The grazers' degree of P homeostasis is modified by Δ_i, defined as the difference between $Q_{Z,i}^{\max}$ and $Q_{Z,i}^{\min}$.

The second differential equation is for the grazer's elemental content, which is a function of intake and losses to either growth or release:

$$\frac{dQ_{Z,i}}{dt} = aIQ_{A,i} - \mu Q_{Z,i} - R_i, \tag{4}$$

where nutrient ingestion follows a linear functional response aI, a is the algal density (cells L^{-1}), I is the clearance rate of the grazer (L $\mathrm{individual}^{-1}$ day^{-1}), and R_i represents the grazer's P or C loss rates (mol $\mathrm{individual}^{-1}$ day^{-1}). Nutrient loss (C or P) depends on nutrient ingestion ($aIQ_{A,i}$) and the demand for those elements based on the relative nutrient content of the grazer:

$$R_i = aIQ_{A,i}\left[1 - e_i\left(\frac{Q_{Z,i}^{\max} - Q_{Z,i}}{Q_{Z,i}^{\max} - Q_{Z,i}^{\min}}\right)\right], \tag{5}$$

where e_i is the maximum accumulation efficiency for nutrient i.

Simulations were conducted with Berkeley Madonna (Macey and Oster 2006). We used the Runge-Kutta 4 method to integrate the homeostatic model. The plastic model is computationally intensive, so we used the autostepsize method. We calculated integral growth rate and homeostasis as described in "Homeostasis and Model Fitting," using the initial and final ($t = 10$) results of simulations.

Taxa and Culture Conditions

We used the experimental framework developed by Sterner and Schwalbach (2001) to examine the integrative ability of seven *Daphnia* species: *Daphnia lumholtzi*, *Daphnia magna*, *Daphnia mendotae*, *Daphnia obtusa*, *Daphnia parvula*, *Daphnia pulicaria*, and *Daphnia pulex*. These seven species fall into all four of the major North American *Daphnia* phylogenetic groups identified by Colbourne and Herbert (1996): the subgenus *Ctenodaphnia* (two species: *D. lumholtzi* and *D. magna*), the *pulex* group (three species: *D. obtusa*, *D. pulicaria*, and *D. pulex*), the *longispina* group (one species: *D. mendotae*), and the "orphan taxa" (one species: *D. parvula*). Six of seven species had been maintained in culture in the R. W. Sterner lab in St. Paul, Minnesota, for several years. *Daphnia lumholtzi* was obtained from L. Wieder (University of Oklahoma).

Twenty-liter stock cultures of *Daphnia* were maintained at room temperature in a COMBO medium (Kilham et al. 1998) modified to contain 40 μM P and 500 μM nitrogen (N). Batch cultures were fed a combination of *Scenedesmus obliquus* and ground dried alfalfa. For the experimental diets, *S. obliquus* was grown in chemostats under P-limited (LP; 1,000 μM N, 5 μM P, dilution = 0.1 day^{-1}) or N-limited (HP; 400 μM N, 80 μM P, dilution = 0.5 day^{-1}) conditions. In experiment 1, LP algae had a mean C : P of 588, while the mean C : P of HP algae was 78 (fig. A1 in the online edition of the *American Naturalist*). In experiment 2, LP algae had a mean C : P of 1,325, while the mean C : P of HP algae was 94. Algal C and P concentrations were determined with a FOSS NIRSystems spectrometer. Calibration equations and validation procedures are described by Hood et al. (2006).

Experiment 1

Twenty-four hours before initiating these experiments, gravid *Daphnia* were removed from batch cultures with a pipette and placed in a jar containing COMBO medium, N (1,000 μM N), and P (80 μM P). Mothers were fed HP algae ad lib. This experiment began with <24-h-old neonates and ended at the first sign of ovary development. Neonates were distributed as follows. Fifteen neonates were placed on glass slides, dried (60°C), weighed, and analyzed for P content as described below. The remaining individuals were distributed among seven treatments. Daphniids were allowed to feed on HP algae for a predetermined number of hours each day (0, 1, 3, 5, 9, 12, or 24 h) and fed on LP algae for the remaining time. Four replicate jars were created for the 100% LP and HP treatments (0- and 24-h treatments), used to measure P homeostasis, while the intermediate treatments had two replicates. When this experiment was repeated with *D. magna* and *D. parvula* (run 2), only two replicate jars were created for the 100% LP and HP treatments. Jars were stocked with 10–20 animals per jar. We varied the density of animals per jar to achieve approximately equal final biomass. Often, there were not enough neonates to start an entire experiment in one day; therefore, the initiation of each experimental bottle was randomized. Neonate samples were collected each day bottles were initiated. Each experimental bottle contained 250 mL of COMBO medium (lacking N and P) and 500 μg C L^{-1} of *S. obliquus.*

To standardize the impact of transferring, animals receiving a constant diet of LP or HP algae were also transferred to a new jar after 12 hours. To remove excess algae during transfers, animals were first placed in a rinse beaker containing basal COMBO and no algal food for at least 1 min. Experimental jars were kept on a tissue culture roller table to keep algae in suspension and were maintained at 20° C under low light in an environmental chamber. Species were run in pairs, with the exception of *D. obtusa* (fig. A1).

Animals were allowed to grow until the first individuals in each container exhibited signs of ovary development (3–6 days). At harvest, animals were removed, placed on a glass slide, and dried at 60°C. Each dried individual was removed from the slide and weighed three times to the nearest 0.1 μg on a microbalance (Mettler UMT2). Several precautions were taken to improve determination of mass in these small individuals. The microbalance was kept in a basement room on a marble table anchored in sand. A Staticmaster Ionizer (Amstat) was used to neutralize static electricity charges. Juvenile growth (μ) was calculated as

$$\mu = \frac{\ln(\text{mass}_{\text{final}}) - \ln(\text{mass}_{\text{initial}})}{\text{time}}, \tag{6}$$

where time was in days.

After weighing, *Daphnia* were transferred to a borosilicate glass tube (2–10 individuals tube^{-1}), ashed (550°C), and analyzed for P content using the molybdate-absorbate method described by DeMott et al. (1998). Phosphorus analyses were run in a 10- or 20-mL reaction tube. To estimate daphniid P : C (molar), we used measured daphniid percent P and assumed that *Daphnia* were 45% C (Andersen and Hessen 1991).

Experiment 2

We used the results of experiment 2 only to help determine the degree of homeostatic regulation for these seven *Daphnia* species. This experiment began with <24-h-old neonates and ended after 72 h. Neonates were distributed as follows. Fifteen neonates were placed on glass slides, dried (60°C), weighed, and analyzed for P content as described above. The remaining individuals were distributed between two treatments, with three replicates per treatment and 10–20 animals per container. Each experimental bottle contained 250 mL of COMBO medium (lacking N and P) and 1 mg C L^{-1} of algae. Daphniids received either HP or LP *S. obliquus.* Daily, animals were transferred to a new bottle containing fresh basal COMBO and algae. During transfers, animals were rinsed in a beaker containing basal COMBO and no algae. Experiments were run on a roller table under low light in an environmental chamber at 20°C. *Daphnia* growth and P content were determined as described above, although a Mettler UMX2 microbalance was used in this experiment.

Homeostasis and Model Fitting

The homeostasis parameter H describes the degree to which a species regulates body elemental content in response to variation in diet (Sterner and Elser 2002). Here, we describe results in terms of $1/H$, which measures stoichiometric flexibility. Higher values of $1/H$ indicate weaker homeostasis (less variation in consumer nutrient content relative to resource nutrient content). We calculated $1/H$ as the slope of the regression line between natural log *Daphnia* P : C and natural log algal P : C. Only *Daphnia* percent P values from 100% LP or HP treatments were used. Differences in $1/H$ among species were examined with a homogeneity-of-slopes test (Statistica).

The parameter H quantifies the stoichiometric regulatory ability of a species for a given resource under a given set of conditions. The value of H measured in any given study might vary with the range of variables considered, the growth conditions, and other environmental factors. For the purposes of this study, we wanted to know the maximum homeostasis that the species might exhibit under conditions similar to our experiments. We therefore chose to use the maximum estimate of stoichiometric homeostasis (H) from our two experiments. Since the relationship between natural log *Daphnia* P : C and natural log algal P : C is linear, differences in algal C : P between experiments are not expected to influence homeostasis estimates (DeMott et al. 1998; Sterner and Elser 2002).

Resource integrators exhibit a saturating relationship between μ and F, which can be fit empirically by a square root function:

$$\mu = \beta_0 + \beta_1 F + \beta_2 \sqrt{F}. \qquad (7)$$

The coefficient β_2 is of particular interest. It defines the curvilinear nature of this nonlinear function. When this square root function is fit to the linear, growth integrator response (fig. 1*b*; growth integrator) β_2 is near 0. β_2 increases as the relationship between μ and F becomes more curvilinear. We use β_2 as a metric of a species' ability to integrate P across diets. The square root model was fit in Statistica (Statsoft). When comparing β_2 among species (or runs), we must assume that all species have a similar β_2 for the relationship between long-term growth and the mean food quality of a mixed diet (fig. 1*b*). Statistical tests used to make additional comparisons are noted in "Results." These tests were conducted in Statistica with $\alpha = 0.05$.

Results

Population Growth Model

Comparison of dynamics from the two models supports our hypothesis that the type of integration is linked to stoichiometric homeostasis. The homeostatic model generates symmetry between the dynamics of population growth and algal P (fig. A2*a* in the online edition of the *American Naturalist*), as predicted for growth integrators (fig. 1*a*). In contrast, the plastic model produces asymmetry between population growth and algal P, as predicted for resource integrators. In the plastic model, temporal variation in growth is characterized by a saturating response following the LP to HP shift and a slow, near-linear decline when shifting from HP to LP algae (fig. A2*a*).

When model results are averaged over the long term (10 days), the homeostatic model produces a linear relationship between μ and F (fig. A2*b*). In contrast, over the long term the plastic model produces a nonlinear relationship between μ and F (fig. A2*b*). The curvilinear nature of this relationship increases with the plasticity (Δ_P) of the grazer (fig. 2*a*), resulting in a positive saturating relationship between resource integration (β_2) and stoichiometric flexibility (1/H; fig. 2*b*). This relationship plateaus at a 1/H of approximately 0.4.

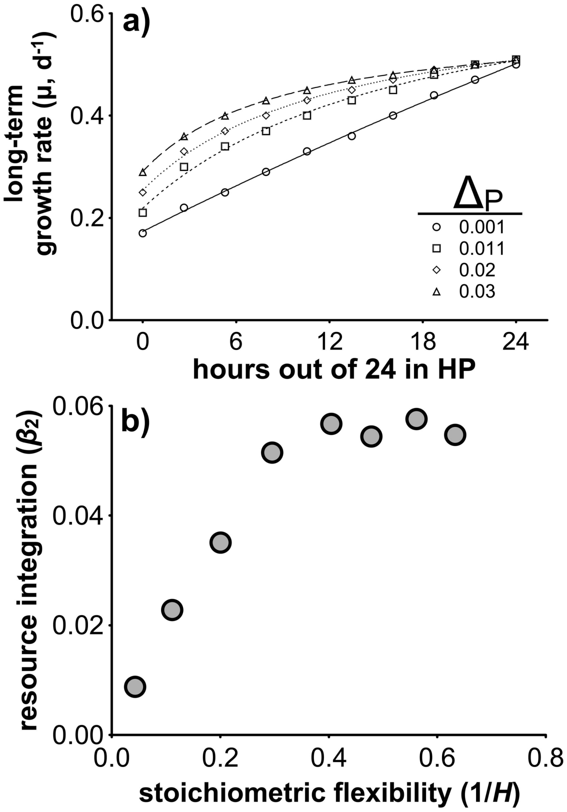

Figure 2: In simulations of the plastic model, the ability to integrate resources (β_2) increases with the plasticity of body phosphorus ($\Delta_P = Q^{\max}_{Z,P} - Q^{\min}_{Z,P}$). *a*, Relationships between long-term growth rate and hours out of 24 in high-phosphorus (HP) algae (F) for model species varying in P plasticity (Δ_P; ρmol P cell^{-1}). *b*, Relationship between resource integration (β_2) and stoichiometric flexibility (1/H) from multiple runs of plastic model, where only Δ_P varied among runs. The homeostasis parameter (1/H) was calculated from simulations where animals consumed 100% LP or HP algae.

Growth and Dietary Phosphorus Integration

All *Daphnia* species grew slower on LP algae than on HP algae (factorial ANOVA diet effect: $F_{1,34} = 23.6$, $P < .0001$; Tukey HSD post hoc: all species, $P < .05$; table 1). Dietary P had the greatest impact on the growth of *Daphnia mendotae* ($\mu_{\text{LP}}\mu_{\text{HP}}^{-1} = 0.06$) and the least impact on *Daphnia pulicaria* (0.68).

Visually, the relationship between juvenile growth (μ) and F for each species can clearly be categorized as linear or nonlinear (fig. 3). Three of the seven species (*Daphnia lumholtzi*, *D. mendotae*, and *Daphnia parvula* [two runs]) exhibited a near-linear relationship between μ and F (fig. 3). For these species, estimates of β_2 were not significantly different from 0 (table 2). These species have little to no capacity for resource integration and could be considered

Table 1: Initial neonate mass as well as the influence of diet on *Daphnia* mass and growth rate (μ)

Species	Neonate mass (μg)	High phosphorus		Low phosphorus	
		Mass (μg)	μ (day^{-1})	Mass (μg)	μ (day^{-1})
Daphnia lumholtzi	3.03 (3.37)	12.44 (.28)	.26 (.00)	7.49 (3.85)	.12 (.06)
Daphnia magna:					
Run 1	10.27 (2.21)	55.53 (5.49)	.28 (.02)	28.17 (3.08)	.17 (.01)
Run 2	4.83 (1.69)	46.6 (.91)	.37 (.02)	12.81 (3.55)	.15 (.05)
Daphnia mendotae	2.71 (1.56)	14.50 (.77)	.29 (.02)	3.37 (.50)	.02 (.01)
Daphnia obtusa	2.11 (.91)	14.07 (1.55)	.33 (.01)	3.98 (.83)	.11 (.01)
Daphnia parvula:					
Run 1	1.38 (.48)	6.06 (.89)	.43 (.04)	2.61 (.56)	.21 (.03)
Run 2	1.42 (.72)	6.03 (NA)	.36 (NA)	2.46 (.56)	.11 (.01)
Daphnia pulex	1.88 (1.15)	22.52 (3.07)	.41 (.01)	5.07 (1.75)	.15 (.04)
Daphnia pulicaria	5.28 (2.41)	24.79 (2.27)	.30 (.02)	15.58 (1.77)	.21 (.01)

Note: Neonate and final masses (±1 SD). Growth rates on low-phosphorus algae (one-way ANOVA; $F_{7,19} = 14.5$, $P < .0001$) and high-phosphorus algae (one-way ANOVA; $F_{7,19} = 6.04$, $P = .0008$) differed among taxa. NA, not applicable.

growth integrators. The other four species (*Daphnia magna*, two runs; *Daphnia obtusa*, *D. pulicaria*, and *Daphnia pulex*) exhibited a nonlinear relationship between μ and F (fig. 3). Estimates of β_2 were significant for these five data sets (table 2), indicating support for resource integration. The capacity for resource integration varied among these four species (fig. 3; table 2).

Both *D. magna* and *D. parvula* runs were replicated in time. The C : P of HP and LP algae did not differ between runs (HP: mean C : P = 75 vs. 77; *t*-test: df = 14, $P = .56$; LP: mean C : P = 517 vs. 619; *t*-test: df = 14, $P = .12$). These two species exhibited qualitatively similar relationships between μ and F in that *D. magna* was found to be a resource integrator in both runs and *D. parvula* was found to be a growth integrator in both runs (fig. 3; table 2). Coefficient fits, however, differed between the runs. The parameter β_2 was higher in the second *D. magna* run (0.0261 vs. 0.1048; fig. 3). The intercept differed between *D. parvula* runs (fig. 3). These differences across runs presumably are due to some unidentified experimental condition or had to do with preexperimental feeding history.

Daphnia *P Content and Homeostasis*

In both experiments 1 and 2, *Daphnia* percent P was generally within the range of previous studies, excluding measurements for *D. pulex* and *D. obtusa* in HP algae as well as *D. mendotae* in LP algae (table 3). Daphniid P content differed among species in both the LP and HP treatments (table 3). The diet-specific P content of *D. parvula* and *D. magna* did not differ significantly between runs (*t*-test; *D. magna* [HP]: $n = 4$, $P = .13$; *D. magna* [LP]: $n = 3$, $P = .09$; *D. parvula* [HP]: $n = 4$, $P = .76$; *D. parvula* [LP]: $n = 4$, $P = .47$).

These seven *Daphnia* species differed in their degree of P flexibility ($1/H$), which ranged from −0.031 to 0.197 (homogeneity of slopes: $F_{6,35} = 22.2$, $P \leq .0001$; table 3). For three of the seven species (*D. lumholtzi*, *D. mendotae*, and *D. parvula*), estimates of $1/H$ were not significantly different from 0 (table 3). These species could be considered strictly homeostatic ($1/H = 0$). Although *D. magna* exhibited the weakest homeostasis ($1/H = 0.197$), all four species with relaxed homeostasis ($P < .05$) varied little in $1/H$ (range: 0.155–0.197).

Two species (*D. obtusa* and *D. mendotae*) showed large differences in their degree of P homeostasis between experiments 1 and 2 (table 3). In experiment 1, *D. mendotae* exhibited weak homeostasis ($1/H = 1.210$), while in experiment 2, this species proved to be strongly homeostatic ($1/H = 0.112$, $P > .05$). In contrast, *D. obtusa* exhibited a negative $1/H$ in experiment 1 ($1/H = -0.643$) and a positive $1/H$ in experiment 2 ($1/H = 0.166$). The potential implications of these differences are discussed below.

Integrative Strategies, Homeostasis, and Life-History Parameters

Simulations of the plastic model suggest that resource integration (β_2) increases linearly with stoichiometric flexibility and then plateaus (fig. 2*b*). The experimental data set suggests, in contrast, that resource integration (β_2) increases nonlinearly with stoichiometric flexibility ($1/H$; fig. 4). Inspection of this data set suggests that the seven daphniids can be categorized into two groups with regard to integration: species with β_2 estimates similar to 0 (growth integrators) and species with a capacity for resource in-

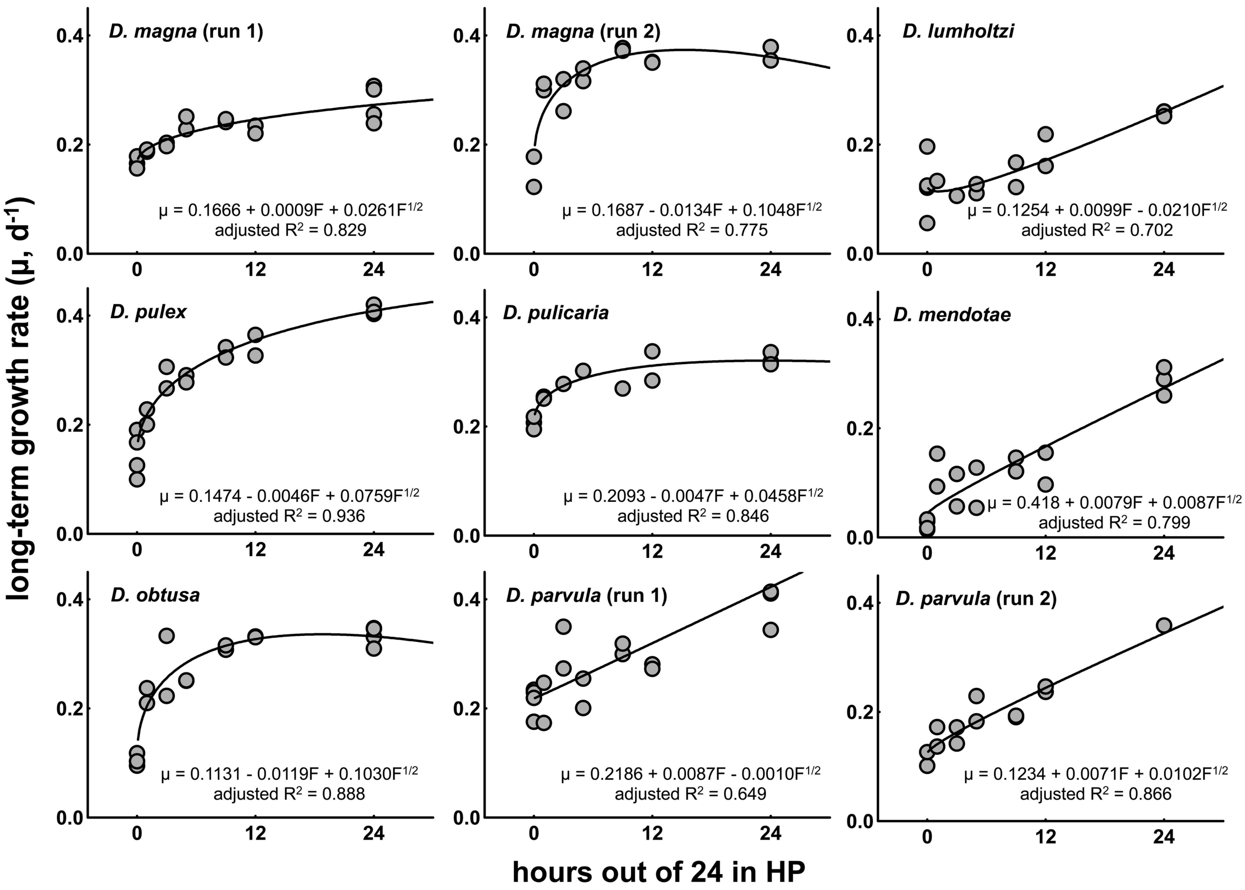

Figure 3: Relationship between long-term growth rate (μ; day $^{-1}$) and hours out of 24 in high-phosphorus (HP) algae (F) for seven *Daphnia* species. *Daphnia parvula* and *Daphnia magna* runs were replicated in time. Runs are designated with run numbers. Only run 1 was used in comparisons.

tegration (fig. 4; table 2). Species with a capacity for resource integration were more stoichiometrically flexible than those categorized as growth integrators (t-test: $t = -3.79$, df $= 5$, $P = .013$; fig. 4). Exclusion of *D. obtusa* and *D. mendotae*, species with greatly divergent $1/H$ estimates, does not influence the nature of this relationship (t-test: $t = -5.90$, df $= 3$, $P = .010$).

Resource integrators did not differ from growth integrators in terms of μ_{HP} (t-test: $n = 5$, $P = .98$), μ_{LP} (t-test: $n = 5$, $P = .60$), percent $\mathrm{P_{HP}}$ (t-test: $n = 5$, $P = .92$), percent $\mathrm{P_{LP}}$ (t-test: $n = 5$, $P = .97$), or sensitivity to P limitation ($\mu_{\mathrm{LP}}\mu_{\mathrm{HP}}^{-1}$; t-test: $n = 5$, $P = .52$). There was a suggestion that growth integrators were smaller than resource integrators, although the difference was not significant at $\alpha = 0.05$ (growth integrators: 11.0 ± 4.2 μg; resource integrators: 29.2 ± 18.2 μg; t-test log mass: $n = 5$, $P = .07$). Furthermore, the homeostasis parameter $1/H$ was not linearly related ($P > .05$) to μ_{HP}, μ_{LP}, percent $\mathrm{P_{HP}}$, percent $\mathrm{P_{LP}}$, or sensitivity to P limitation.

Discussion

Animals must often consume diets of varying quality, resulting in a temporally heterogeneous diet. However, there has been little consideration of how long-term growth in a heterogeneous environment relates to component growth rates associated with patches of different nutritional quality. The most common approach uses diet-specific growth rates to predict long-term growth (Iversen 1974; White 1993; Urabe et al. 1997), thus implicitly assuming that animals integrate instantaneous growth rates across diets. Alternatively, animals may temporally mix resources across diets (i.e., integrate resources, not growth) and exhibit higher growth rates than expected on the basis of component diets (fig. 1).

The seven *Daphnia* species examined in this study exhibited wide variation in their capacity for resource integration. Three species (*Daphnia lumholtzi*, *Daphnia mendotae*, and *Daphnia parvula*) exhibited little to no capacity

Table 2: Estimates of the relationship between long-term growth (μ) and hours in high-phosphorus algae

Species	Adjusted R^2	β_0	β_1	β_2
Daphnia lumholtzi	.702	.1254 (.0166)*	.0099 (.0033)*	−.0210 (.0164)
Daphnia magna:				
Run 1	.775	.1666 (.0109)*	.0009 (.0019)	.0261 (.0100)*
Run 2	.775	.1687 (.0199)*	−.0134 (.0034)*	.1048 (.0177)*
Daphnia mendotae	.799	.0418 (.0195)*	.0079 (.0038)	.0087 (.0192)
Daphnia obtusa	.888	.1131 (.0155)*	−.0119 (.0027)*	.1030 (.0143)*
Daphnia parvula:				
Run 1	.649	.2186 (.0266)*	.0087 (.0050)	−.0010 (.0258)
Run 2	.866	.1234 (.0156)*	.0071 (.0031)	.0102 (.0145)
Daphnia pulicaria	.846	.2093 (.0098)*	−.0047 (.0019)*	.0458 (.0096)*
Daphnia pulex	.936	.1474 (.0117)*	−.0046 (.0023)	.0759 (.0115)*

Note: Coefficient estimates for the polynomial relationship between μ and F (slope ± 1 SE) for each run.
* $P < .05$.

for resource integration (fig. 4). For simplicity, we consider these species growth integrators because their estimates of β_2 are not statistically different from 0 (table 2). The other four species (*Daphnia magna*, *Daphnia obtusa*, *Daphnia pulicaria*, and *Daphnia pulex*) exhibited variation in their capacity for resource integration. We found a positive nonlinear relationship between resource integration and stoichiometric flexibility (fig. 4). Growth integrators were more homeostatic than resource integrators. These results may suggest that resource integration requires a threshold level of stoichiometric flexibility. Yet our model simulations suggest that resource integration should increase linearly with stoichiometric flexibility to a plateau (fig. 2*b*).

The prevalence of nutrient storage and wide variation in N and P homeostasis observed in invertebrates (Persson et al. 2010) suggests that strategies across a continuum of resource integration efficiency may be common. Thus, understanding how to scale growth rates (and, by implication, fitness) from component growth rates in individual habitats up to complex mosaics of high- and low-quality patches could potentially be extremely difficult, but our results indicate that a relatively simple parameter, the degree of stoichiometric homeostasis, will be useful in determining how to scale fitness from patches to the landscape.

Another approach for determining the influence of patch heterogeneity on fitness is provided by the geometric framework developed by Raubenheimer, Simpson, and colleagues (see review in Behmer 2009). This framework uses state-space plots to determine how animals mix complementary diets (e.g., a high-protein diet and a high-carbohydrate diet) to maximize fitness. This body of work clearly demonstrates that many diverse animals can identify high-quality food and act to mix diets to optimize nutrient intake as well as growth, when allowed to feed ad lib. This approach does not, however, explicitly identify relationships between patch use and long-term fitness. In this study, *Daphnia* were not allowed to choose or optimize diet mixtures. Instead, we examined a wide range of predetermined mixtures (i.e., hours in HP algae), allowing us to predict the relationship between patch use and long-term fitness across a wide range of landscapes. Terrestrial insects may use both growth and resource integrator strategies, although not the same strategy for all nutrients. For example, Raubenheimer and Jones (2006) fed German cockroaches (*Blatella germanica*) diets high in either carbohydrates or proteins. German cockroaches store excess carbohydrates and proteins when the nutrients are available, suggesting the potential for integration of both nutrients. Furthermore, Raubenheimer and Jones (2006) argue that the ability to store excess carbohydrates is common among insect species while the ability to store excess proteins may be rare. Resource integration may thus be a common strategy for coping with environmental heterogeneity in carbohydrates but not in proteins.

Phosphorus Homeostasis

Our results show that regulation of P homeostasis varies widely among *Daphnia* species, supporting DeMott and Pape's (2005) findings. In our study, three species (*D. lumholtzi*, *D. mendotae*, and *D. parvula*) were identified as strongly homeostatic, while four other species (*D. magna*, *D. obtusa*, *D. pulex*, and *D. pulicaria*) exhibited weaker P homeostasis. Our measurements are, in general terms, consistent with several studies, although we did identify one discrepancy. Published laboratory studies with *D. magna*, *D. pulex*, and *D. pulicaria* also indicate weak P homeostasis ($1/H$: 0.1–0.2; Plath and Boersma 2001; DeMott and Pape 2005; Ferrão Filho et al. 2007), while DeMott and Pape (2005) describe *D. mendotae* as strongly homeostatic. In contrast, *D. parvula* exhibited weak P ho-

Table 3: Stoichiometric flexibility (1/*H*) and the influence of diet on *Daphnia* phosphorus (P) content

	Experiment 1			Experiment 2			
Species	P_{HP} (%)	P_{LP} (%)	Slope	P_{HP} (%)	P_{LP} (%)	Slope	1/*H*
Daphnia lumholtzi	1.58 (.12)	1.45 (.04)	.036 (.034)	1.88 (.17)	1.25 (.13)	.111 (.042)*	.036
Daphnia magna:							
Run 1	1.57 (.06)	.89 (.00)	.293 (.026)*	1.79 (.16)	.93 (.07)	.197 (.035)*	.197
Run 2	1.18 (.30)	1.90 (.54)	−.231 (.194)				
Daphnia mendotae	1.06 (.15)	.10 (.02)	1.210 (.150)*	1.23 (.06)	1.12 (.17)	.112 (.057)	.112
Daphnia obtusa	.64 (.24)	2.02 (.23)	−.643 (.207)*	1.36 (.09)	.95 (.05)	.166 (.056)*	.166
Daphnia parvula:							
Run 1	1.94 (.09)	2.06 (.14)	−.031 (.044)	1.34 (.14)	1.17 (.15)	.038 (.079)	−.031
Run 2	1.83 (NA)	1.80 (.40)	.005 (.170)				
Daphnia pulex	2.45 (.15)	.81 (.14)	.572 (.101)*	1.66 (.19)	1.01 (.08)	.155 (.022)*	.155
Daphnia pulicaria	1.50 (.10)	1.00 (.06)	.193 (.038)*	1.36 (.02)	.92 (.02)	.207 (.046)*	.193

Note: *Daphnia* P content (μg P μg dry mass^{-1}; ±1 SE) in the low-phosphorus (LP) and high-phosphorus (HP) treatments and the slope (±1 SE) of the relationship between ln *Daphnia* phosphorus : carbon (P : C) ratio and ln algal P : C. Results from both experiments 1 and 2 are shown. The degree of stoichiometric flexibility (1/*H*) is the maximum degree of homeostasis (*H*) exhibited between experiments. Daphnid P content differed among species when fed both LP algae (one-way ANOVA; $F_{7,18} = 28.9$, $P < .0001$) and HP algae ($F_{7,19} = 11.5$, $P < .0001$). NA, not applicable.

* $P < .05$.

meostasis in one laboratory study (1/*H* =~ 0.1, DeMott and Pape 2005), while our results suggest strong homeostasis. Discrepancies among studies are not particularly surprising. Phosphorus homeostasis is not a species-level trait; instead, it varies within species among clones (Jeyasingh et al. 2009) and with food quantity (Ferrão Filho et al. 2007).

Our decision to use the maximum homeostasis from experiments 1 and 2 affects the interpretation of our results, though the main conclusions do not rest on this point. The homeostasis parameter 1/*H* differed greatly between experiments for only two species: *D. mendotae* and *D. obtusa*. Exclusion of these two species does not significantly alter our central finding that the capacity for resource integration increases with stoichiometric flexibility. Furthermore, the mathematical models also support the link between nature of integration and stoichiometric homeostasis.

Mechanistic Explanations for Resource Integration

Two mechanisms could be responsible for resource integration: luxury uptake or variation in nutrient use efficiency (NUE). These mechanisms are not mutually exclusive and may at times work in concert to maximize resource integration. Luxury uptake has been defined in multiple ways (Ågren 2008). Here we define luxury uptake operationally as nutrient assimilation in excess of immediate growth requirements (Elrifi and Turpin 1985).

Organisms with the capacity for luxury uptake and the subsequent storage of excess nutrients can use nutrient reserves to supplement growth on a low-quality diet, allowing an organism to be a resource integrator. A wide variety of organisms, ranging from autotrophs to invertebrates and mammals, are capable of resource (i.e., protein, carbohydrate, phosphorus) storage and therefore resource integration (Elrifi and Turpin 1985; Khoshmanesh et al. 2002; Woods et al. 2002; Barboza and Parker 2006; Lee et al. 2006; Raubenheimer and Jones 2006), though

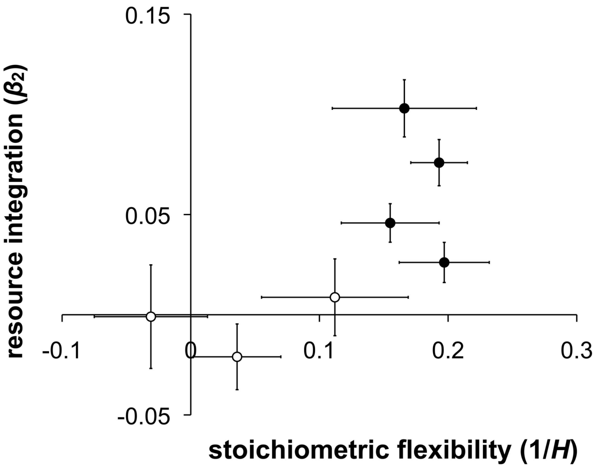

Figure 4: Resource integration (β_2) increases nonlinearly with stoichiometric flexibility (1/*H*). Species with a significant capacity (β_2 $P < .05$) for resource integration were the most stoichiometrically flexible (*t*-test; $n = 5$, $P = .013$). Filled circles indicate species with significant model fits for both resource integration and stoichiometric flexibility (*Daphnia magna*, *Daphnia obtusa*, *Daphnia pulex*, and *Daphnia pulicaria*; $P < .05$). Open circles indicate species with insignificant fits for both models (*Daphnia lumholtzi*, *Daphnia mendotae*, and *Daphnia parvula*; $P > .05$). Error bars are 1 SE.

the capacity for storage varies widely among both groups and resources.

Luxury uptake may not always be available as a strategy. Some species may not have a significant capacity for luxury uptake or may reside in environments where resources are never available in excess. However, resource integration can also occur in the absence of luxury uptake, when the NUE of a nutrient-limited species negatively scales with diet quality and growth rate. Here we define NUE as the carbon to nutrient ratio of an organism's body (e.g., C : P), which will reflect the carbon to nutrient ratio of new growth. It is common for NUE to vary with dietary or environmental variables (Sterner and Elser 2002). Phosphorus use efficiency (PUE), for example, can be a growth rate–dependent parameter. When P is limiting, PUE is inversely related to growth rate (Elser et al. 2003). This relationship results from the tripartite linkage between growth, RNA, and body P described by the growth rate hypothesis (Elser et al. 1996). This tripartite linkage can lead to resource integration.

In heterogeneous environments with low- and high-quality patches, these linkages allow for resource integration. When a species with a variable NUE moves from a high-quality to a low-quality patch (e.g., HP to LP), its high nutrient content and growth rate are not sustainable in the new patch. Over time, NUE increases as the organisms' growth rate and nutrient content decline. In this scenario, the difference between the organism's nutrient content in the high-quality and low-quality patches can be considered excess nutrients, although those nutrients were not excess when incorporated. These newly excess nutrients—made available by diet-induced changes in NUE—supplement growth on the low-quality patch, leading to resource integration. This mechanism of resource integration may be common among weakly homeostatic species, at least when P is the focal resource. A wide variety of organisms, ranging from bacteria to both aquatic and terrestrial invertebrates (DeMott et al. 1998; Elser et al. 2003; Fink and Von Elert 2006), exhibit the positive relationship between growth and body P required for this resource integration mechanism.

The two physiological mechanisms described above appear to be widespread across heterotroph groups, suggesting, although not proving, that resource integration may be a common response to environmental heterogeneity. It is more difficult to estimate the prevalence of the growth integration strategy, which requires strict homeostasis, since estimates of $1/H$ are rare for heterotrophs other than *Daphnia* (Persson et al. 2010). Nevertheless, the distribution of strategies within the genus *Daphnia* could suggest that both strategies are common.

Integration Strategies, Competition, and Ecosystem Dynamics

The strategic and physiological differences between growth and resource integrators provide a framework for understanding competition in heterogeneous systems. When temporally mixing diets, resource integrators use nutrients available across complex landscapes more efficiently than do growth integrators. This increased efficiency should allow resource integrators to potentially outcompete growth integrators in variable environments or heterogeneous landscapes. Yet the ability to integrate a resource instead of growth does not inherently lead to dominance in variable environments. Rapidly growing species or those insensitive to nutrient limitation may dominate in both homogeneous and heterogeneous landscapes, regardless of integration strategy. We did not identify any clear trade-offs between resource integration and growth rates in constant environments. In the absence of any trade-off, resource integration would be favored in any heterogeneous environment. It has no clear drawback, while there appears to be no trade-off associated with weak homeostasis.

The linkage between integration strategy and stoichiometric homeostasis implies that resource and growth integrators may play different roles in food webs and nutrient cycles. Strictly homeostatic growth integrators will release nutrients when available in excess while retaining nutrients when scarce, consistent with past theoretical treatments (Sterner 1990). Resource integrators fit differently into nutrient cycles. These species store nutrients when available in excess, releasing nutrients only once storage reservoirs are full. By sequestering nutrients in tissue, resource integrators may decrease, relative to growth integrators, the availability of labile nutrients as well as the quality of their own food. Storage could lengthen the periods of autotroph and heterotroph nutrient limitation in consumer-resource cycles (Andersen et al. 2004). Furthermore, since the nutrient stoichiometry of resource integrators may be highly variable, the presence of these species in food webs could more likely lead to nutrient limitation of predators (Malzahn et al. 2007).

Significance

In spite of widespread acknowledgment of the occurrence of spatial and temporal heterogeneity, few studies have examined how an animal's instantaneous response to patch quality scales into its long-term performance within a complex landscape. Here, using mathematical simulations and *Daphnia* as a model group, we explored the function linking patch quality and frequency of patch use with long-term growth. We suggest that there is a continuum of responses, beginning with growth integrators and ending with resource integrators capable of mixing all nutrients in excess across diets. Resource integrators should have higher long-term resource use efficiency than growth integrators. Thus, all else being equal, resource integrators should outcompete growth integrators in heterogeneous environments, where resource quality varies among patches. A species' capacity for resource integration can be predicted by the degree of stoichiometric flexibility. Furthermore, the degree of resource integration will influence a species' fitness as well as the role it plays in food webs and nutrient cycles.

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