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Feeding in the frequency domain: Coarser-grained environments increase consumer sensitivity to resource variability, covariance and phase

Apostolos-Manuel Koussoroplis^{*1,2}, Svenja Schällicke^{*1}, Michael Raatz^{*1,3}, Moritz Bach¹, and Alexander Wacker^{1,4}

¹Theoretical Aquatic Ecology and Ecophysiology group, Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany.

²Aquatic Food Web Interactions group (I.R.T.A), Microorganisms Genome and Environment Lab (L.M.G.E.) UMR CNRS 6023, Université Clermont Auvergne, Aubière, France.

³Department of Evolutionary Theory, Max Planck Institute for Evolutionary Biology, Plön, Germany.

⁴Animal Ecology, Zoological Institute and Museum, University of Greifswald, Greifswald, Germany.

*These authors contributed equally.

[†]Corresponding author:

Université Clermont Auvergne, L.M.G.E. UMR CNRS 6023
Campus Universitaire des Cézeaux
1 Impasse Amélie Murat
TSA 60026 CS 60026
63178 AUBIERE Cedex
FRANCE
a-manuel.koussoroplis@uca.fr
Phone: +33 4 73 40 77 51

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Abstract

Theory predicts that resource variability hinders consumer performance. How this effect depends on the temporal structure of resource fluctuations encountered by individuals remains poorly understood. Combining modelling and growth experiments with *Daphnia magna* we decompose the complexity of resource fluctuations and test the effect of resource variance, supply peak timing (i.e. phase) and co-limiting resource covariance along a gradient from high to low frequencies reflecting fine to coarse-grained environments. Our results show that resource storage can buffer growth at high frequencies, but yields a sensitivity of growth to resource peak timing at lower ones. When two resources covary, negative covariance causes stronger growth depression at low frequencies. However, negative covariance might be beneficial at intermediate frequencies, an effect that can be explained by digestive acclimation. Our study provides a mechanistic basis for understanding how alterations of the environmental grain size affect consumers experiencing variable nutritional quality in nature.

Introduction

The nutritional traits of prey such as the composition of limiting resources or secondary metabolites strongly influence consumer performance and population dynamics (Sternern & Elser 2002; Simpson & Raubenheimer 2012; Hunter 2016; Sperfeld *et al.* 2016; Raatz *et al.* 2017). Spatiotemporal variability in the nutritional quality of food resources is inherent to natural consumer-resource systems (Orians & Jones 2001; Park *et al.* 2004; Junker & Cross 2014; Grosbois *et al.* 2016), and most consumers face intense and frequent fluctuations in food quality during their lifetime. Accumulating evidence shows that such resource variability strongly influences consumers at the individual (Stockhoff 1993; Hood & Sternern 2010; Pearse *et al.* 2018), population, and community level (Underwood 2004; Riolo *et al.* 2015) and may have far-reaching implications such as the control of herbivore pest populations in agroecosystems (McArt & Thaler 2013; Wetzel *et al.* 2016). Resource variability effects manifest as a deviation between performance achieved under fluctuating resource supply and performance that would be achieved under the same average, yet constant resource supply (*variance effect*, **Fig. 1A**). If performance is a non-linear saturating function of resource concentration, non-linear averaging predicts that performance should decrease with resource variability, proportionally to resource variance and function curvature (Jensen's inequality (Ruel & Ayres 1999; Wetzel *et al.* 2016)).

To date, studies on resource variability focused on single nutritional traits (Carlotti *et al.* 2010; Hood & Sternern 2010; Wagner *et al.* 2017). Yet, consumer performance can be simultaneously driven by several nutritional traits of their food (*e.g.* concentrations of various mineral and biochemical resources or secondary metabolites), a situation known as co-limitation (Sperfeld *et al.* 2012, 2016). Hence, when feeding in nutritionally variable environments, consumers need to acquire, store and use multiple co-limiting resources which might, or might not, co-occur temporally and spatially. Non-linear averaging predicts that,

when resources act non-additively, consumers should perform differently in positive and negative covariance scenarios despite temporal means and variances of the co-limiting resources being equal (*covariance effect*, Koussoroplis & Wacker 2016; **Fig. 1B**). Given the propensity of co-limiting resources acting non-additively on consumer performance (Simpson & Raubenheimer 2012; Sperfeld *et al.* 2016), the importance of resource variability for consumers cannot be addressed without considering the interplay of co-limitation and the spatiotemporal covariance of the co-limiting resources in the landscape.

Independent of whether the consumer is sessile in a dynamic environment (e.g. bivalves in tidal estuarine systems) or mobile in a heterogeneous landscape (e.g. daily vertically migrating zooplankton), spatial and temporal nutritional variance and covariance are always experienced by the consumer as temporal fluctuations in resource supply. Hence, changes in spatial or temporal contrasts of resource availability influence the variance and covariance of resource supply, whereas the grain size of the environment (i.e. size or duration of food patches), the motility and life span, as well as the foraging behavior of the consumer influence the frequency and phase of the perceived fluctuations. While the fluctuation frequency and phase of the nutritional environment can be highly different across consumer taxa and ecological contexts, non-linear averaging approaches cannot, by definition, accommodate their potential effects on consumer performance (Kingsolver & Woods 2016; Wetzel & Thaler 2016; Kremer *et al.* 2018; Pearse *et al.* 2018). Thus, for the same resource variance or covariance, differences in resource supply frequency or phase could yield performances that differ from non-linear averaging predictions (Koussoroplis *et al.* 2017a). In order to construct a general theory on the importance of resource variability for consumers, we thus need to understand the responses to resource supply fluctuation frequency and phase as well as the physiological mechanism mediating them.

In most living organisms, assimilated resources are first stored into a metabolically inactive pool (hereafter *reserves*) and subsequently mobilized and used for maintenance, growth, or reproduction (Kooijman 2010). Such reserves may buffer the effects of high frequency resource fluctuations on performance (hereafter *reserve effect*) (Muller & Nisbet 2000; Fujiwara *et al.* 2003; Hood & Sterner 2010). Furthermore, many organisms dynamically acclimate to fluctuating resources by adjusting nutrient extraction and transport through gut enzyme modifications (Karasov *et al.* 2011; Koussoroplis *et al.* 2017b), thereby improving the assimilation efficiency of the most limiting resource (Clissold *et al.* 2010; Urabe *et al.* 2018). However, acclimation processes may also have negative consequences if they involve energetic costs (Wetzel & Thaler 2016) or if acclimation lags behind the changes in environmental conditions (Niehaus *et al.* 2012; Kingsolver & Woods 2016; Koussoroplis *et al.* 2017a; Kremer *et al.* 2018). To date, the roles of reserves and acclimation in mediating organismal responses to fluctuating environments are studied in isolation. Yet, the combined effects of the two processes on resource-determined growth, where they are likely to co-occur, remains unstudied.

Here, we test the hypothesis that for the same mean and variance of resource fluctuations, environments with different temporal patterns (i.e. resource covariance, frequency, and phase, **Fig. 1C**) lead to altered consumer growth responses that do not necessarily comply with non-linear averaging predictions. We used a two-resource Dynamic Energy Budget (DEB) model (**Fig. 2**) to predict the somatic growth of a consumer facing constant versus fluctuating resource supply and investigate how performance differences are mediated by the temporal structure of resource availability. The effects of the temporal patterns in limiting and co-limiting resource supply on somatic growth were tested experimentally using juvenile *Daphnia magna* reared on variable phosphorus (P) and cholesterol supply. Our study offers theoretical and empirical evidence that the temporal

structure of resource availability can strongly decrease consumer growth in fluctuating environments and provides a mechanistic understanding of such negative effects.

Materials and Methods

Design of the study

For the same total duration, modelled or experimental organisms are exposed either to different constant resource supply conditions (**Fig. 1A,B**; open and black filled circles), or to sequences of resource regimes alternating high and low supply of a single or two co-limiting resources, thereby experiencing the same resource supply mean and variance over time. Constant treatments are used to obtain non-linear averaging predictions of consumer growth (**Fig. 1A,B**; filled grey, red, and blue circles). Fluctuating resource treatments are used to study variance in a single resource alternating in low or high supply, while the other resource is kept at constant high supply (**Fig. 1A**), or covariance in two co-limiting resources alternating in their supply, resulting in negative or positive covariance (**Fig. 1B**). Fluctuations are applied at different fluctuation frequencies (i.e. time spans of high or low supply) and different phases (i.e. starting with high or low supply) (**Fig. 1C**).

Model structure

Based on DEB Theory (Kooijman 2010), we constructed an ordinary differential equation (ODE) model that predicts the juvenile somatic growth of an organism (**Tab. 1**). The three important aspects of the model are (i) co-limitation by two interactively essential resources, (ii) independent storage of these resources in two reserves and (iii) regulation of assimilation efforts depending on the relative filling of the reserves with a trade-off between the two resources.

The state variables are the structural volume of the organism V , the resource density in the reserve E_i (i = resource 1 or 2) and the assimilation effort ϕ , which determines the

assimilation efficiencies for the two resources $\varepsilon_i(\phi)$ (**Fig. 2**). Resources are assimilated from the food proportionally to the available resource concentrations, the organism's surface and the assimilation efficiency. Assimilates are then added to the reserves at rates p_{Ai} . Reserves are consumed at rates p_{Ci} , proportionally to their density. The synthesizing unit (SU) (Kooijman 1998) combines the two consumption fluxes at a fixed ratio with rate p_{SU} , which, after subtracting maintenance costs p_M , results in structural growth. If influxes to the SU are imbalanced, excessive resources are rejected with rate p_{Ri} , of which a fraction returns to the reserves while the rest is excreted. Fluxes in and out of the reserves are expressed as resource density fluxes in units of resources per structural volume per time.

We assume that the production of nutrient-specific digestive enzymes is energetically costly and that it involves trade-offs hindering the capacity of the consumer to maximize assimilation efficiency for all resources simultaneously (Zera & Harshman 2001). We therefore implemented a trade-off in the assimilation efficiencies of the two co-limiting resources (*see Appendix 1, Fig. A1, A2* for further details). Along this trade-off the organism allocates the assimilation effort (i.e. production of nutrient-specific enzymes) towards the most limiting resource as a compensatory mechanism maintaining nutrient uptake homeostasis (Clissold *et al.* 2010). Evidence suggests that in invertebrates such digestive processes are controlled by the nutrient status of the hemolymph (Bede *et al.* 2007).

Accordingly, in the model, the allocation of assimilation effort is controlled by the balance of resources in the reserves. The adjustments of the assimilation effort are not immediate. We therefore implemented a characteristic switching time that determines the speed at which an organism acclimates to changed resource conditions (*see Appendix 1, Fig. A1, A2* for further details). The model equations and parameter estimates are provided in **Table 1**.

Obtaining modelled growth rates

The resulting system of ODEs is numerically integrated using the *odeint* package from the *Scipy* library (Jones *et al.* 2001) in Python (version 3.7) for the different constant or fluctuation treatments. Starting from low initial volume and low, balanced reserve densities, the unsaturated increase in structural volume within the first four days yields an estimate for the somatic growth rate of juveniles that may be compared to experimental observations. Different parameter combinations, which represent limiting cases of (i) no reserves, no variable assimilation (null model), (ii) no variable assimilation, (iii) no reserves, and (iv) the full model with reserves and variable assimilation, give rise to submodels that combine the three important model components (i.e. Reserve, Acclimation, SU). Reserves are excluded by increasing the reserve conductance 1000-fold. At such high values, the resources are stored for a negligibly short time-interval before being passed on to the SU, thereby preventing any significant reserve build-up. Acclimation is excluded by fixing the assimilation efficiencies at the intermediate assimilation effort $\phi = 0.5$ along the trade-off curve. A sensitivity analysis for the three most influential parameters is presented in **Appendix 2 (Fig. A3-5)**.

Experiments

Stock cultures of *D. magna* were kept as in (Koussoroplis & Wacker 2016). For the experiments, we used P-replete (SynP+) and P-deficient (SynP-) *Synechococcus elongatus* (SAG 89.79), a non-toxic cyanobacterium lacking essential sterols, using the culture protocol described in (Lukas *et al.* 2011). By mixing SynP+ and SynP- cultures the appropriate P:C ratios of food suspensions were obtained. Cholesterol containing liposomes were produced following the protocol described in (Wacker & Martin-Creuzburg 2012) and supplemented to the food suspensions to obtain desired cholesterol concentrations.

Third-clutch juveniles of *D. magna* (< 24 h old) were born on *S. elongatus* with low resource supply (1.25 mmol P molC⁻¹, 0.25 µg cholesterol mgC⁻¹). In the constant treatments daphnids experienced either constant high or low P (6.66; 1.25 mmol molC⁻¹) each in

combination with constant high or low cholesterol (8; 0.25 $\mu\text{g mgC}^{-1}$), or average conditions (3.95 mmol P molC⁻¹; 4.125 $\mu\text{g cholesterol mg C}^{-1}$). In the variance treatments high and low supply of either P or cholesterol fluctuated, while the other resource was at constant high supply. In the covariance treatments high concentrations coincided or alternated, respectively for positive and negative covariance. For a total duration of 4 days, three different fluctuation frequencies of the resource supply (0.25 d⁻¹, 0.5 d⁻¹, 1 d⁻¹, corresponding to 1.25, 2.5, and 5 cycles per generation of approximately 5 days, respectively (Giebelhausen & Lampert 2001)) were applied for variance and covariance treatments, where animals experienced different fluctuation phases, i.e. either high or low supply in the respective varying resource(s) first. Each treatment consisted of four replicates with six juvenile *D. magna* per replicate. The cholesterol variance experiment was performed twice and the data were pooled resulting in eight replicates. The experiments were conducted at 20°C in the dark using glass beakers filled with 200 ml of food suspensions prepared with ADaM medium (Klüttgen *et al.* 1994). Food suspensions of *S. elongatus* with targeted resource concentrations were prepared daily. Food quantity was kept constant at *ad-libitum* levels (2 mgC L⁻¹). Twice (for 1 d⁻¹ fluctuation treatments) or at least once per day (for constant, 0.25 d⁻¹ and 0.5 d⁻¹ fluctuation treatments) daphnids were transferred into renewed food suspensions to avoid food quantity limitation and to simulate (co)variance in P and cholesterol. Initial dry mass (M_0) of animals was determined using three subsamples of 10 juveniles ($\pm 1\mu\text{g}$, CP2P; Sartorius, Göttingen, Germany). Somatic growth rate g (d⁻¹) was calculated as increase in dry mass using the equation

$$g = \frac{\ln M_T - \ln M_0}{T},$$

where T is the duration of the experiment (4 days) and M_T the final dry mass of animals.

Data analysis

To test for effects of fluctuation frequency and phase (variance experiments) or fluctuation frequency and covariance direction (covariance experiment) on growth, two-way ANOVAs were applied followed by Tukey HSD post-hoc tests. A nested-design two-way ANOVA was used to additionally test for effects of fluctuation phase nested within positive and negative covariance in the covariance experiment. Here, only the lowest fluctuation frequency of 0.25 d^{-1} was considered. Means and associated 95% confidence intervals (CI) were estimated using a bootstrapping approach with 1000 repetitions (Efron & Tibshirani 1993). We tested whether our observations in the various fluctuation treatments are significantly different from the growth rate under constant average resource supply (i.e. $g(\bar{R})$, $g(\bar{R}_1, \bar{R}_2)$) and from that predicted by non-linear averaging (i.e. $\overline{g(R)}$, $\overline{g(R_1, R_2)}_+$, $\overline{g(R_1, R_2)}_-$), by comparing their respective CI. A significant difference was concluded in the absence of overlap.

Results

Reserve dynamics predict fluctuation frequency-dependent effects of resource supply variability and phase on consumer growth

With the SU alone, the model behaves as predicted by non-linear averaging, that is, frequency independent (**Figs. 3A and 4A**). However, including reserves increases growth across all fluctuation frequencies compared to the null model, most dominantly at high frequencies (**Fig. 3B and Fig. 4B**). As fluctuation frequency increases growth increases from the non-linear average prediction $\overline{g(R)}$ to the growth predicted from constant average resource supply $g(\bar{R})$ in the variance treatments. In the covariance treatments, growth moves from the non-linear average prediction for positive, $\overline{g(R_1, R_2)}_+$, and negative covariance, $\overline{g(R_1, R_2)}_-$, to the growth predicted for average co-limiting resource supply, $g(\bar{R}_1, \bar{R}_2)$. This model version also predicts a resource phase effect since growth is higher when the organism experiences a high

resource supply first in the nutritional sequence. This phase effect is strong at low fluctuation frequencies and decreases with increasing fluctuation frequency.

Acclimation dynamics yield maladaptive consumer responses at high resource fluctuation frequencies

In our model, acclimation acts when only one resource fluctuates or the two resources are fluctuating asynchronously, i.e. in the variance (**Fig. 3C**) and negative covariance treatments (**Fig. 4C**), respectively. The positive effect of acclimation on growth becomes apparent at low frequencies and on the non-linear average predictions $\overline{g(R)}$ and $\overline{g(R_1, R_2)}$, where growth rates increase compared to the null model (e.g. **Fig. 3A** vs. **Fig. 3C**). For higher fluctuation frequencies the lag of acclimation dynamics behind nutritional fluctuations becomes too strong for organisms to fully acclimate. This leads to a decrease in growth below $\overline{g(R)}$ and $\overline{g(R_1, R_2)}$. As resource fluctuations become very fast, assimilation efficiencies remain in an intermediate, non-specialized range and growth collapses towards the null model predictions.

Combining reserves and acclimation yields inversions in the direction of the covariance effect and frequency gradient

Including storage and acclimation combines the traits of the two previous model versions, thereby enhancing growth relative to the null model both at the highest and lowest fluctuation frequencies (**Fig. 3D** and **Fig. 4D**). At the intermediate frequency range, however, the full model predicts a novel pattern where growth under single resource variance or negative covariance can surpass that expected under constant conditions ($g(\bar{R})$ or $g(\bar{R}_1, \bar{R}_2)$, respectively) (**Fig. 3D** and **Fig. 4D**). For fluctuations in both resources, this yields an inversion of the covariance effect where the growth rates for negatively covarying resources exceed those for positively covarying ones, as opposed to the non-linear average predictions (**Fig. 4D**). As for the reserves model version, the full model also predicts changes in phase effect size along the frequency gradient. However, as we parametrized both resources

identically, phase affects growth only in the positive covariance scenario, where an initially low resource supply decreases growth at low fluctuation frequencies compared to initially high resources (**Fig. 4D**). These model outcomes are robust for broad parameter ranges (**Appendix 2, Fig. A3-5**).

Experiments confirm the effect of fluctuation frequency, phase effects and maladaptive responses

We found a strong agreement between experimental results and most predictions of the full model. In the experiment with fluctuating cholesterol supply, growth rates were affected both by fluctuation frequency (two-way ANOVA, $F_{2,41} = 20.21$, $p < 0.001$) and phase ($F_{1,41} = 41.17$, $p < 0.001$). As predicted, there were no growth differences between different fluctuation phases at high frequencies (**Fig. 3E**), where growth rates were comparable to $g(\bar{R})$. At low frequencies, however, the growth rate was more reduced (by 30.0%) when exposed to low cholesterol concentrations first, than when experiencing high concentrations first (11.8% reduction) (interaction: $F_{2,41} = 9.56$, $p < 0.001$).

In the experiment with fluctuating P supply, growth rates were only marginally affected by fluctuation frequency (two-way ANOVA, $F_{2,18} = 2.63$, $p = 0.10$; **Fig. 3F**). A marginal interaction between frequency and phase ($F_{2,18} = 3.01$, $p = 0.07$) suggests the predicted increase in growth differences between the two phases from no difference at the high frequency to 17.4% difference at the low frequency. In agreement with the model, growth rates were generally lower when animals experienced low P supply first (factor fluctuation phase, $F_{1,18} = 33.86$, $p < 0.001$): When exposed to high P supply first, growth rates were high across all fluctuation frequencies tested and did not differ from $g(\bar{R})$ (**Fig. 3F**). When experiencing low P supply first, growth rates decreased by 8.4%, 12.8% and 18.4% with decreasing fluctuation frequency compared to $g(\bar{R})$, a pattern also predicted by the model. At the 0.25 d^{-1} frequency growth rates were even 11.5% lower than $\overline{g(\bar{R})}$ (**Fig. 3F**).

Lower growth rates than $\overline{g(R)}$ are also predicted by the full model for certain parameter ranges (**Appendix 2, Fig. A6**).

Experiments partially confirm covariance effect inversion along the frequency gradient

The experiment confirmed the majority of model predictions for the two resource covariance scenarios (**Fig. 4E**). Similar to the model predictions, the frequency effect was less pronounced for positive (from 7.3% to 15.0% lower growth rates) than for negative covariance (from 1.3% to 23.7% lower growth rates), which is supported by a significant interaction of fluctuation frequency and covariance direction ($F_{2,18} = 15.14$, $p < 0.001$). As predicted, we observed an inversion of covariance effects; at the 0.25 d^{-1} frequency, negative covariance yielded a stronger growth rate decrease (23.7%) relative to $\overline{g(R_1, R_2)}$ than positive covariance (10.5%) (Tukey HSD, $p < 0.05$), whereas at the 1 d^{-1} frequency the decrease was stronger for positive covariance (14.9%) than for negative covariance (1.7%) (Tukey HSD, $p < 0.05$). The overshoot of growth rates above $\overline{g(R_1, R_2)}$ was not observed at the frequencies applied in the experiment. Consistent with the model prediction, growth was affected by fluctuation phase under positive covariance (18.7 % difference) (nested ANOVA, $F_{2,12} = 38.07$, $p < 0.001$; Tukey HSD, $p < 0.001$), but was similar under negative covariance (Tukey HSD, $p = 0.09$), which was tested experimentally for the 0.25 d^{-1} frequency (**Fig. 4E**).

Discussion

Our results highlight the importance of fluctuation frequency for the effect of nutritional variability on consumer's growth. The nutritional variability constraint becomes stronger in coarser-grained environments where perceived nutritional quality fluctuates slowly. As such, our study confirms the hypothesis that non-linear averaging cannot predict nutritional variability effects across all fluctuation frequencies. The simulations suggest that non-linear averages are accurate only when fluctuation frequency is slow enough to empty the

reserves and allow for a full dietary acclimation of the consumer. We further show that the effect of resource phase and covariance on growth increases for lower frequencies. This finding stresses the need to consider the timing of resource peaks and the spatiotemporal correlation of co-limiting resources in order to understand how nutritionally complex environments constrain consumers. Below we discuss the causes of the observed patterns and their ecological implications.

Non-linear averages and consumer performance in nutritionally variable environments

In a seminal study, (Hood & Sterner 2010) showed that the growth responses of different *Daphnia* species exposed to a given P fluctuation pattern fall within a gradient ranging from “growth integration” to “resource integration”. These two terms correspond to the non-linear average, $\overline{g(R)}$ and the growth under average constant conditions $g(\bar{R})$, respectively (Koussoroplis *et al.* 2017a). While these terms are very intuitive, using them to define a strategy *vis-à-vis* dietary variability can be misleading (Hood & Sterner 2010; Wagner *et al.* 2017). As shown in our study, whether an animal exhibits growth or resource integration depends on the frequency at which resources fluctuate.

Animals typically experience variability at a multitude of temporal scales. For growing herbivorous zooplankton, these range from diurnal variability induced by vertical or horizontal migration between regions differing in seston quality (Park *et al.* 2004) to daily or few days variability driven by changes in the physiology and species composition of phytoplankton communities (Jonasdottir *et al.* 1995; Martin-Platero *et al.* 2018). Here, we show that within this range the same species can exhibit either growth or resource integration. Hence, the question is not whether an organism *is* a growth integrator (i.e. whether non-linear averaging can predict growth) or not. Instead we have to ask under which conditions organisms are *acting* as such and if these conditions actually occur in their natural habitats. As

we will discuss below, answering this question requires to understand how physiology shapes growth responses to the various scales at which resources fluctuate.

Nutritional variability effects: Reserves and acclimation shape growth responses across frequencies

Reserves explain the decrease in somatic growth with decreasing fluctuation frequency as we observed in our experiments. Hence, reserve capacity likely determines whether an organism will respond as a *resource* or a *growth integrator* when exposed to a given resource fluctuation frequency. Furthermore, a higher reserve capacity (i.e. lower reserve conductance (Kooijman 2010)) translates into higher flexibility in somatic stoichiometric or biochemical composition and encompasses the capability to grow as fast as $g(\bar{R})$ over a wider range of decreasing fluctuation frequencies. Hood & Sterner (2010) found that, when exposed to the same P fluctuation pattern, *Daphnia* species with more flexible C:P stoichiometry tend towards resource integration (or $g(\bar{R})$). These stoichiometric flexibility differences suggest that *Daphnia* species differ in their P reserve capacity. Here, our model predicts that an increase in reserve capacity should come at the cost of a decrease in growth rate under constant or nearly constant resource supply (very high frequency fluctuations). More data is needed to quantify interspecific variability in reserve capacity and to clarify whether it involves trade-offs.

As for reserves, the capacity to acclimate to environmental changes might not be beneficial under all circumstances. The existence of trade-offs, such as the one we implemented in our model, offers a general explanation for frequently observed maladaptive responses across taxa. The model predicts that maladaptive responses in digestive acclimation decrease growth when the resource fluctuations are too slow for reserves to buffer, yet too fast for acclimation to track. Under such circumstances, maladaptive acclimation can yield lower growth rates than a growth integrator would achieve (i.e. below the non-linear average,

$\overline{g(R)}$), a situation we also observed in our P experiment. On the other hand, the consumer benefits from acclimation when fluctuations are significantly slower than the time required for full acclimation. In the model, this benefit manifests as a higher non-linear average than what would be achieved without acclimation. Acclimation capacities are unlikely to evolve if they regularly yield maladaptive responses (Botero *et al.* 2015). An intriguing hypothesis is that in the historical environment of a consumer with acclimation capacity, the frequencies leading to non-linear average growth rates are more common than those yielding a growth rate below the non-linear average.

Phase effect: When obtaining resources earlier in life is advantageous

Size differences during juvenile stages can drive intraspecific interactions (dominance or cannibalism) and may determine survival in the case of gape-size-limited predation. We show that for the same temporal mean and variance in cholesterol and P supply *Daphnia* neonates released within a high quality food patch achieve larger body sizes during the course of our experiments than those experiencing high quality later. This phase-dependent growth rate difference becomes significant when the nutritional conditions persist for 1 day (0.5 d^{-1} frequency), a duration that roughly corresponds to 20% of a generation time (ca. 5 days at 20°C and saturating food, Giebelhausen & Lampert 2001). Hence, relatively modest differences in dietary history can generate substantial intra-individual differences in size-at-age of juveniles experiencing the same dietary temporal mean and variance. In accordance with our findings, insect larvae experiencing high quality food early in ontogeny can better cope with low quality resources later (Stockhoff 1992; Stoyenoff *et al.* 1994). Our results suggest that the importance of fluctuation phase should increase in coarser-grained environments. Furthermore, our model predicts that at least during the juvenile period this phase effect becomes stronger with higher reserve capacity (**Appendix Fig. A4, but see** Fujiwara *et al.* 2003 for longer periods). This context specificity of phase effects could

partially explain why selection of oviposition sites that insure early access to high quality food to offspring is not systematically observed across species (Wetzel & Strong 2015).

Covariance effect: Linking prey diversity and consumer performance across environmental grain sizes

In terrestrial systems, negative relationships between plant species diversity and herbivore density are frequently observed (Crutsinger 2006; McArt & Thaler 2013). Recent hypotheses explain this pattern by the fact that plant diversity translates into nutritional variance. By moving from one leaf or host plant to another, insect herbivores experience the plants' inherent intra- and inter-individual variance in nutrient contents (Orians & Jones 2001; Herrera 2017). Because of non-linear effects (Wetzel *et al.* 2016) and the need to continuously acclimate to the variable plant biochemistry (Wetzel & Thaler 2016; Pearse *et al.* 2018) herbivore growth is constrained (*variance hypothesis*). On the other hand, experimental studies, typically at the phytoplankton-zooplankton interface, show that plant diversity improves consumer growth (Striebel *et al.* 2012; Marzetz *et al.* 2017; Urabe *et al.* 2018). The hypothesized explanation is that diverse prey assemblages translate into increased biochemical diversity which enables herbivores to obtain the optimal blend of co-limiting resources (Marzetz *et al.* 2017) while diluting potential secondary metabolites (Simpson & Raubenheimer 2012) (*co-limitation hypothesis*). Both of the above hypotheses are potentially correct. Nevertheless, the two are boundary cases that either assume the absence of nutritional co-limitation (*variance hypothesis*) or a very-fine grained and well-mixed nutritional environment thus excluding temporal nutritional variance (*co-limitation hypothesis*). Covariance effects can accommodate both the nutritional variance that is inherent to coarser-grained environments and nutritional co-limitation. This allows merging negative and positive prey diversity effects on consumers within a common framework. Furthermore, covariance effects account for the way prey species in a community differ in terms of nutritional quality.

Negative covariance describes a situation when prey species in a community differ mostly in terms of co-limiting resource *ratios* whereas in a positive covariance situation species have similar ratios but vary mostly in terms of co-limiting resource *concentrations*.

Our study provides the first proof of principle for dietary covariance effects (but see (Chambers *et al.* 1996)). While we find the expected change of covariance effects with fluctuation frequency, this change is more complex than anticipated (Koussoroplis *et al.* 2017a). An important and entirely novel result in our study is the possibility of inversions in the direction of the covariance effect along a frequency gradient. Our model suggest that this inversion could be explained by the interaction between reserve and imperfect acclimation dynamics. Yet, the inversion pattern in the model presents some differences compared to the experimental results suggesting that certain aspects of the acclimation dynamics might be missing. Future work should explore how potential acclimation to absolute resource supply, rather than ratios, or the inclusion of energetic acclimation costs can improve the match of the predictions with our results.

Conclusions

In this study, we measured the qualitative differences in the growth response along a gradient of dietary fluctuation frequencies. We demonstrated that these frequencies modulate the effect sizes of resource supply variance, phase and covariance. Our model shows how physiological mechanisms (i.e. reserves, acclimation), which may have evolved in response to different temporal scales of variation, can be coupled. This is a necessary step to understand organismal response to fluctuating environments (Dillon *et al.* 2016). The good agreement with our experimental results suggests that the model indeed captures the most important aspects. In order to achieve this mechanistic understanding, however, we had to trade control over complexity. Thus, extrapolation of our findings to a natural context requires caution. Unlike our experiments and simulations, in which resource supply fluctuates periodically,

natural nutritional noise is more likely to be stochastic. Consumers should therefore simultaneously experience nutritional variance over a wide range of superimposed frequencies. Overall, our results suggest that lower frequencies need less amplitude to yield an effect on growth than high frequencies. Yet, whether and how the superimposed frequencies that compose a stochastic signal act on growth remains unanswered (Dillon *et al.* 2016), and presents fertile grounds for future investigations.

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Data accessibility

The experimental data as well as a Python script allowing to reproduce Fig. 3 and Fig. 4 are available at [figshare link here].

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State variables				
Symbol	Description	Differential equation	Initial condition	Unit
ϕ	Assimilation effort	$\frac{d\phi}{dt} = \frac{1}{\tau}(\phi_T(x) - \phi)$	0.5	1
E_i	Reserve density	$\frac{dE_i}{dt} = p_{Ai} - p_{Ci} + \kappa p_{Ri} - (p_{SU} - p_M) E_i$	10^{-11}	mol mm ⁻³
V	Structural volume	$\frac{dV}{dt} = (p_{SU} - p_M) V$	0.008	mm ³
Functions				
Symbol	Description	Equation		
$\phi_T(x)$	Target assimilation effort at reserve balance $x = \frac{y_1 E_1}{y_2 E_2}$	$\phi_T(x) = \begin{cases} -\frac{1}{2}x^\gamma + 1, & x \leq 1 \\ \frac{1}{2}x^{-\gamma}, & x > 1 \end{cases}$		
$\varepsilon_i(\phi)$	Assimilation efficiency	$\begin{aligned} \varepsilon_1 &= \phi^\alpha (\varepsilon_{max} - \varepsilon_{min}) + \varepsilon_{min} \\ \varepsilon_2 &= (1 - \phi)^\alpha (\varepsilon_{max} - \varepsilon_{min}) + \varepsilon_{min} \end{aligned}$		
Fluxes				
Name	Equation			Unit
Assimilation flux	$p_{Ai} = p_{Am} \varepsilon_i n_i V^{-1/3}$			mol mm ⁻³ d ⁻¹
Catabolic flux	$p_{Ci} = u E_i V^{-1/3}$			mol mm ⁻³ d ⁻¹
Outflow of SU	$p_{SU} = \frac{1}{\frac{1}{g_{max}} + \frac{1}{y_1 p_{C1}} + \frac{1}{y_2 p_{C2}} - \frac{1}{y_1 p_{C1} + y_2 p_{C2}}}$			d ⁻¹
Rejection flux	$p_{Ri} = \begin{cases} p_{Ci} - p_{SU}/y_i, & p_{Ci} - p_{SU}/y_i > 0 \\ 0, & p_{Ci} - p_{SU}/y_i \leq 0 \end{cases}$			mol mm ⁻³ d ⁻¹
Maintenance flux ^a	$p_M = 0.3 \text{ d}^{-1}$			d ⁻¹
Parameters - fixed				
Symbol	Description	Value		
τ	characteristic switching time of assimilation ^b	0.1 d		
α	curvature of assimilation trade-off	3		
γ	sensitivity for reserve balance	5		
n_i	resource concentrations in the food	$7 \times 10^{-3} \text{ mol molC}^{-1}$ (high cond.) $3 \times 10^{-4} \text{ mol molC}^{-1}$ (low cond.)		
p_{Am}	maximum ingestion rate ^c	$4 \times 10^{-6} \text{ molC mm}^{-2} \text{ d}^{-1}$		
y_i	yield of structural volume per mole resource i ^d	$1.5 \times 10^8 \text{ mm}^3 \text{ mol}^{-1}$		
g_{max}	maximum volume-specific growth rate ^e	0.6 d ⁻¹		
κ	fraction of resources rejected by the SU and returned to the reserves	0.3		
Parameters - submodel-specific (null model, with storage, with acclimation, full model)				
ε_{max}	maximum assimilation efficiency	0.2, 0.2, 0.9, 0.9		
ε_{min}	minimum assimilation efficiency	0.2, 0.2, 0.1, 0.1		
u	Reserve conductance ^f	1000, 1, 1000, 1 mm d ⁻¹		

592

593 **Table 1: Model equations and parameter estimates.** The model is loosely parametrized for *Daphnia*, when
594 available, published values are given. All other values are set within reasonable biological ranges. ^a from
595 (Vanoverbeke 2008); ^b inferred from (Koussoroplis *et al.* 2017b); ^c calculated from (Koussoroplis & Wacker
596 2016); ^d inferred from (Sperfeld & Wacker 2009) for cholesterol; ^e Authors' personal observation on the *D.*
597 *magna* clone used; ^f slightly modified from AmP *Daphnia magna* version 2016/02/04
598 bio.vu.nl/thb/deb/deblab/add_my_pet/.

Figure legends

Figure 1: Hypotheses. (A) For single resource limitation, non-linear averaging predicts that the average growth rate of a consumer experiencing fluctuating supply in a limiting resource R , $\overline{g(R)}$, should be lower than the growth rate of a consumer experiencing a constant resource environment with same average resource conditions, $g(\bar{R})$. Consumer growth rate should decrease with increasing resource fluctuation amplitude. (B) When expanding to two co-limiting resources (R_1, R_2) , the average growth rate of a consumer experiencing positively covarying co-limiting resources, $\overline{g(R_1, R_2)_+}$, should be higher than that of a consumer experiencing negative covariance, $\overline{g(R_1, R_2)_-}$. (C) Because of reserve and acclimation effects (see text), the realized growth and therefore the exactitude of non-linear averaging predictions (panels A and B) should be modulated by the resource fluctuation phase and frequency (for simplicity, only single resource cases are depicted).

Figure 2: Dynamic Energy Budget (DEB) model. Arrows indicate fluxes and rectangles indicate the state variables. Numbered circles indicate implemented physiological mechanisms: (i) The organism has the capacity to acclimate by adjusting its assimilation effort towards the resource that has the lower reserves (is most limiting). The acclimation process involves a time lag and implies a trade-off shown in the left panel below. (ii) The organism has a reserve compartment for each resource that buffers the amplitude of higher frequency fluctuations in ingested resources (middle panel below). (iii) The synthesizing unit (SU) merges the resource fluxes that are liberated from the reserves into new biomass with a fixed resource ratio. The rate at which the SU produces biomass from the reserves depends on the magnitude and the balance of the mobilized resources fluxes. The SU was implemented such that under constant resource conditions, the two resources act as interactively essential resources thereby enabling resource covariance effects.

Figure 3: Effects of frequency and phase for fluctuations of one limiting resource. (A-D)

Model results for the somatic growth rate of a consumer for the four different submodels. The dark grey horizontal lines are the predictions for growth under the same average constant resource supply, $g(\bar{R})$, whereas the lighter horizontal line is the non-linear averaging prediction of growth under variable resource supply, $\overline{g(R)}$ (see Fig. 1A). (E-F) Experimental observations of juvenile growth rate of *Daphnia magna* (mean \pm 95% confidence interval, C.I.) under (E) fluctuating cholesterol or (F) phosphorus supply, with different starting conditions representing different fluctuation phases experienced after birth. The darker shaded area is the 95% confidence interval (C.I.) of $g(\bar{R})$. The lighter shaded area is the 95% C.I. of $\overline{g(R)}$. The other (non-fluctuating) resource (phosphorus or cholesterol in the experiments) is kept at saturating supply.

Figure 4: Effects of frequency, phase, and covariance for fluctuations of two co-limiting resources. (A-D)

Modelled somatic growth rate of a consumer for the different submodels with positively (blue) or negatively (red) covarying supply in the two co-limiting resources. The black horizontal line shows the predicted growth under the same average constant resource supply, $g(\bar{R}_1, \bar{R}_2)$, whereas the red and blue lines are the non-linear averaging predictions of growth under variable resource supply, $\overline{g(R_1, R_2)}_{+/-}$ (see Fig. 1B). (E) Experimentally observed juvenile growth rate of *Daphnia magna* (mean \pm 95% C.I.) under positively or negatively covarying phosphorus and cholesterol supply. The combined effect of fluctuation phase and covariance was tested experimentally for 0.25 d^{-1} fluctuations. The grey shaded area is the 95% C.I. of $g(\bar{R}_1, \bar{R}_2)$. Colored areas are the 95% C.I. of $\overline{g(R_1, R_2)}_+$ (blue) and $\overline{g(R_1, R_2)}_-$ (red). Filled circles denote high starting resource supply, whereas open circles indicate low resource supply experienced after birth.

Figures

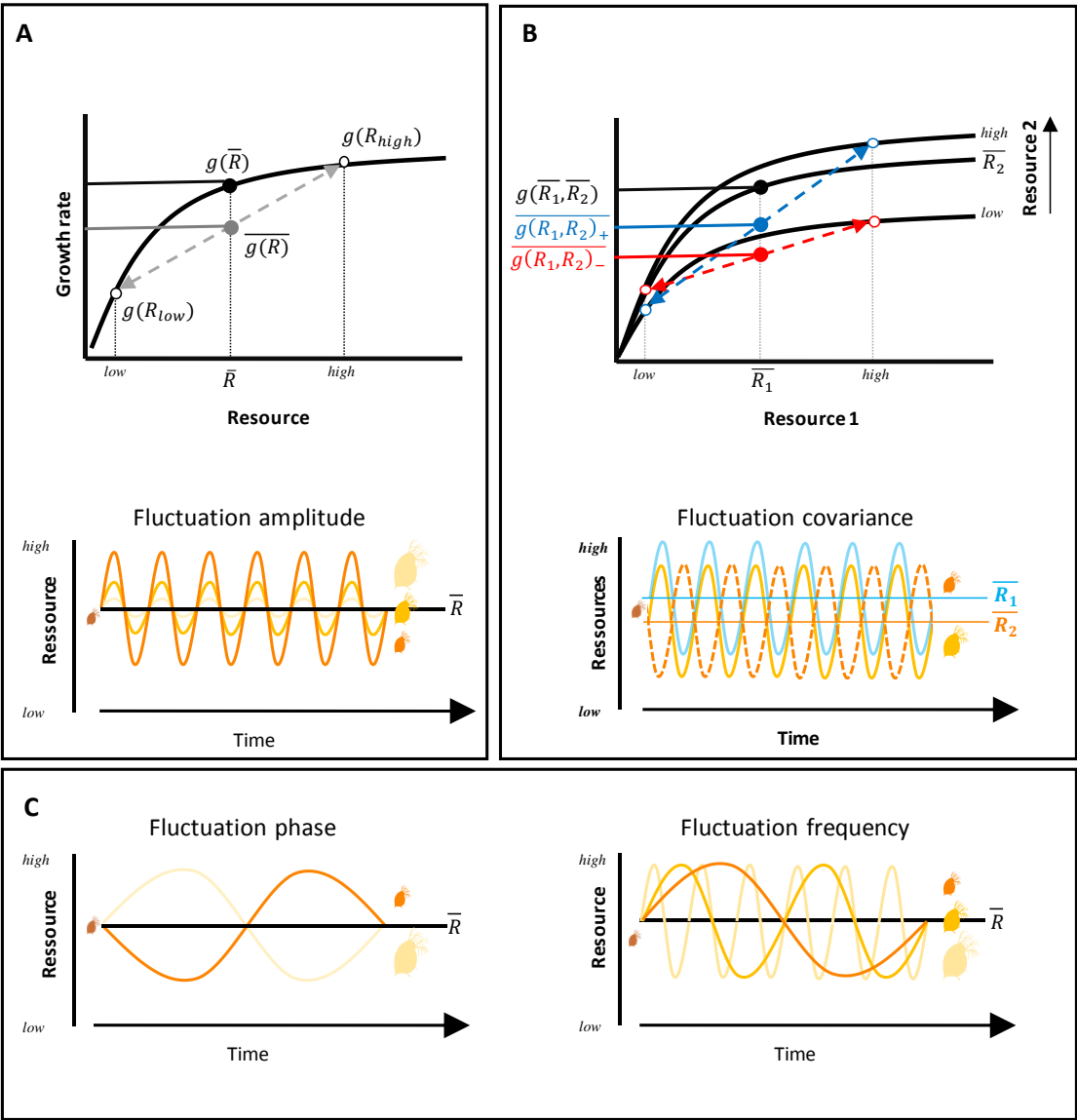


Figure 1

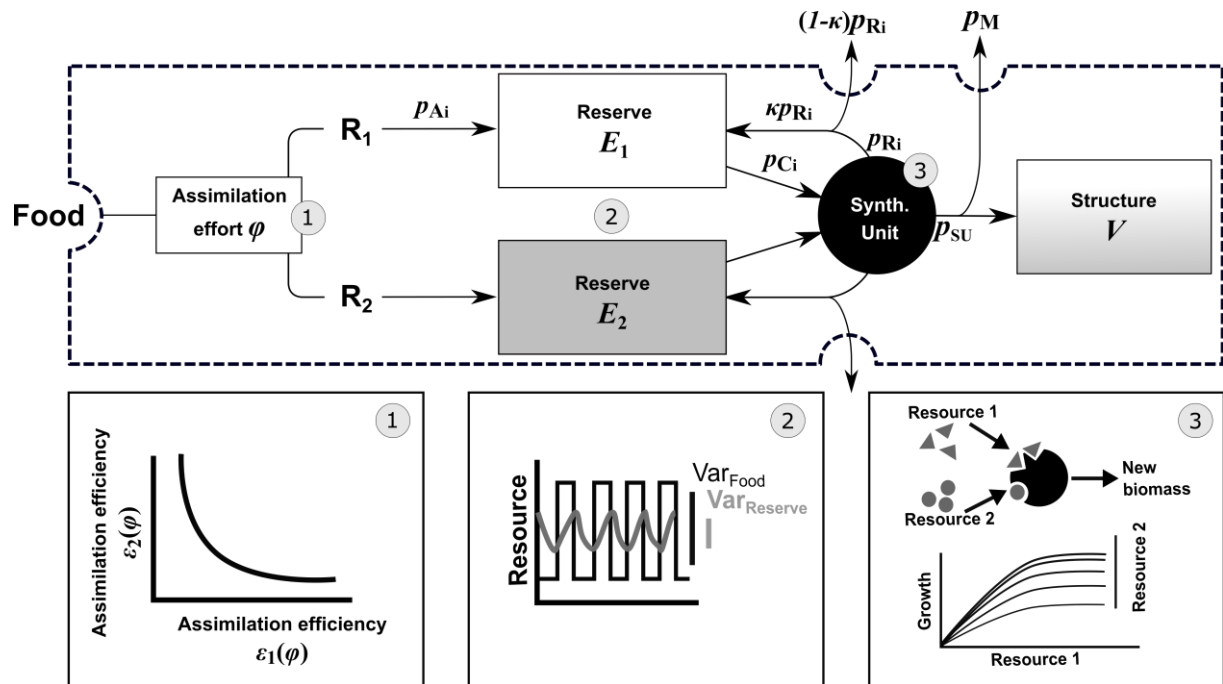


Figure 2

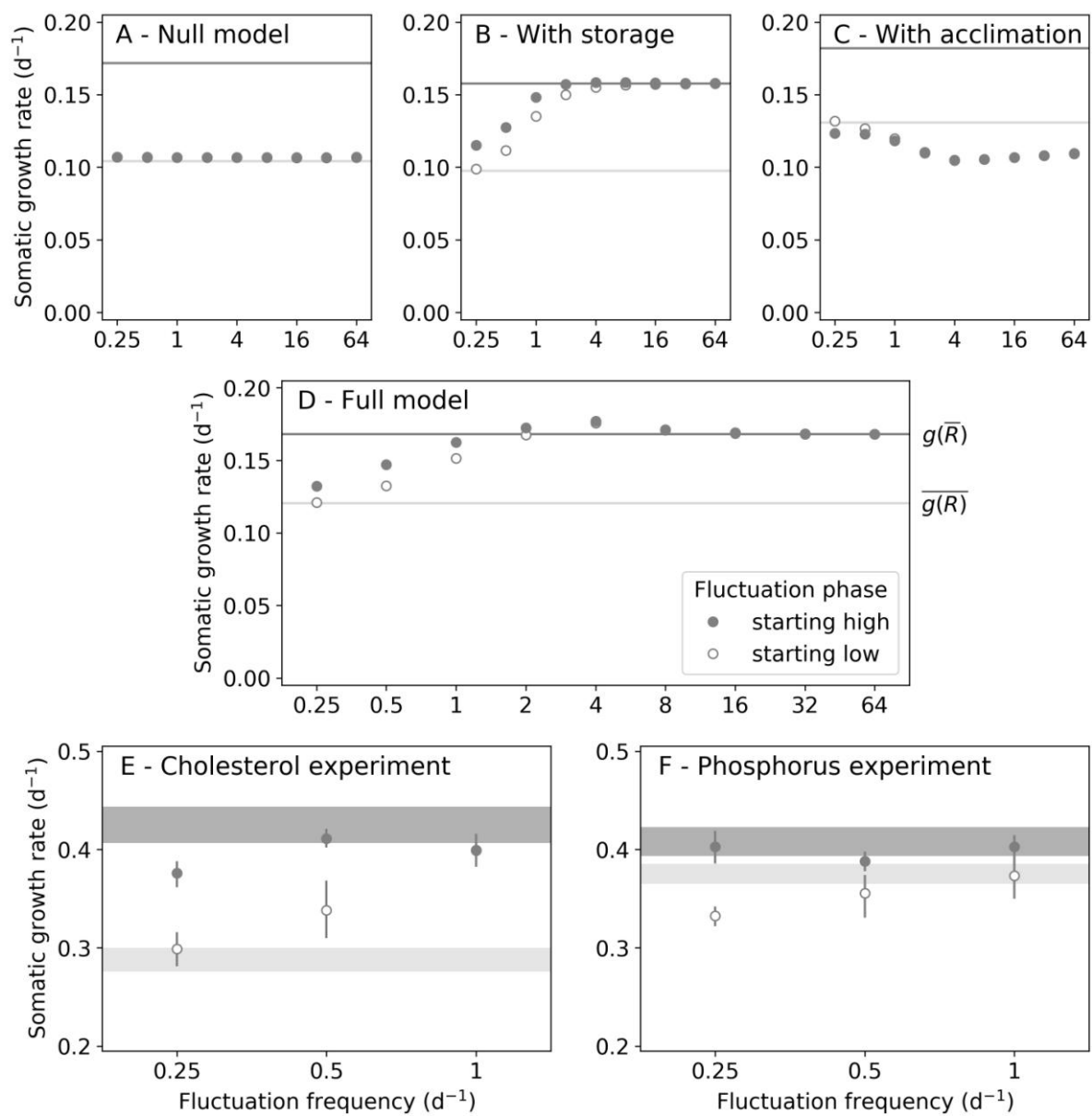


Figure 3

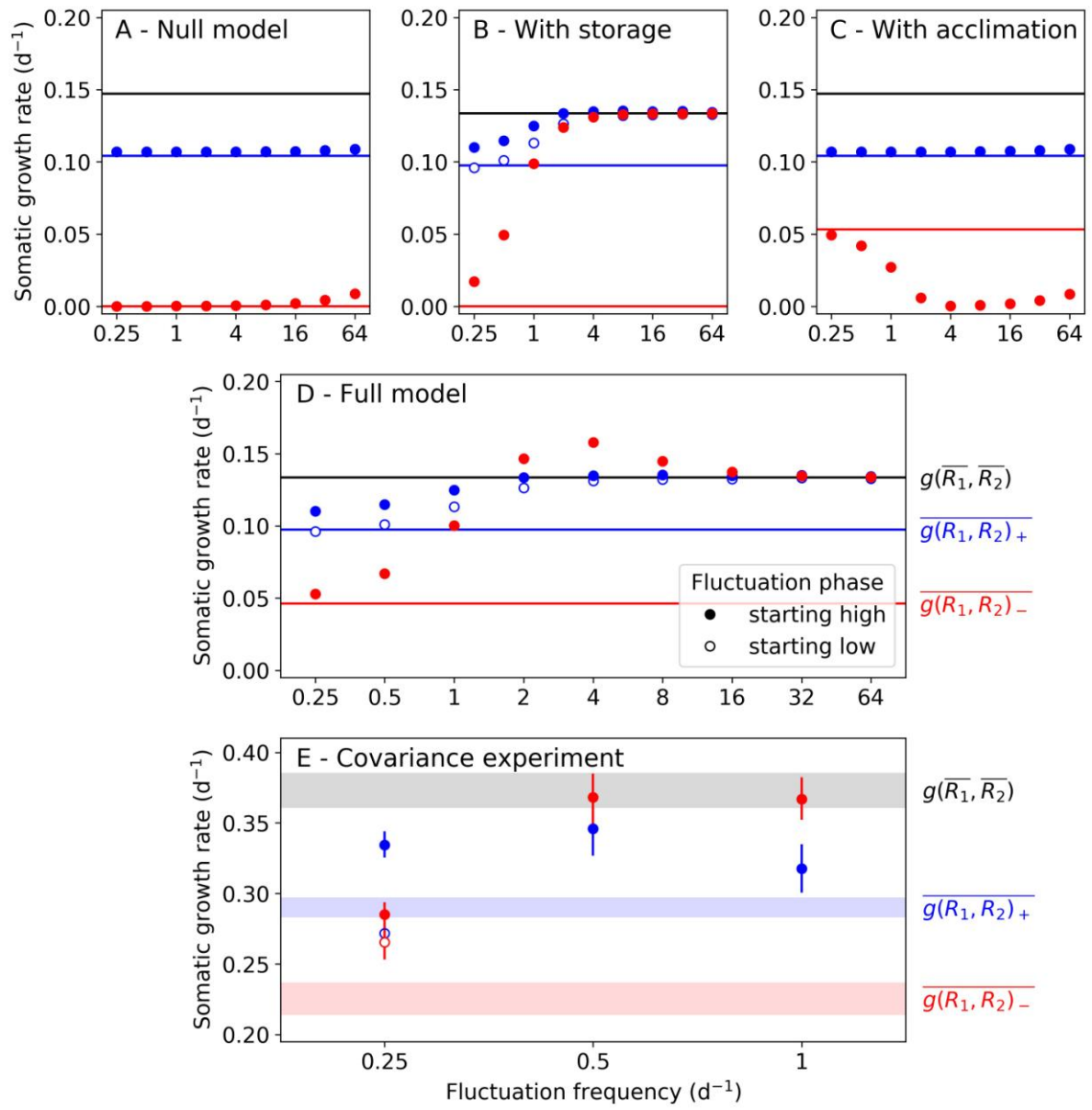


Figure 4