

## NOTES

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### Diel integration of food quality by *Daphnia*: Luxury consumption by a freshwater planktonic herbivore

**Abstract**—The chemical content of living algal food is an important determinant of zooplankton herbivore fitness. Previous studies have restricted diets to a single food type presented over multiple body mass turnover times; these have established that phosphorus content is one factor closely associated with growth of some zooplankton. In nature, however, algal P content and other potentially important dimensions to food quality vary in space and time. It would be unlikely for a grazing animal to experience a single constant food type over a major portion of its life. Many grazers likely experience diel variation in food quality associated with their vertical migration through nutritional gradients. It is not known how long-term growth under fluctuating food relates to growth rates expected for single, constant food types. We tested whether grazers could integrate over daily variation in their food and thus realize body growth rates higher than would be expected from growth determined on single constant food types alone. We found that *Daphnia magna* grow near maximal rates when exposed to high-quality food for half or less of the day. These results suggest that nutritional gradients associated with vertical migration bear close examination. They also strongly suggest that some form of diel P storage in zooplankton, a form of luxury consumption, occurs, and allows for integration over temporal variation in supply of this essential dietary ingredient.

The growth of planktonic herbivores is determined by multiple environmental factors, including physical dimensions such as temperature (Patalas 1990), chemical parameters such as pH (Sierszen and Frost 1990) or [Ca] (Tessier and Horwitz 1990), infochemicals produced by other organisms (Stibor 1992), and the quantity and quality of available food. Phosphorus content is one component of food quality in freshwater zooplankton (Gulati and DeMott 1997; Sterner and Schulz 1998). *Daphnia* growth correlates with algal P content (Sterner 1993; Sterner and Hessen 1994; Gulati and DeMott 1997). P supplement experiments (Urabe et al. 1997; DeMott 1998) have shown this to be a direct causal relationship of P limitation, not a spurious correlation of P with a specific biochemical such as a fatty acid as has been asserted (Brett 1993; Müller-Navarra 1995). Correlations between seston P content and zooplankton community structure (Hessen 1992; Hassett et al. 1997; DeMott and Gulati 1999) and between seston P content and zooplankton P content (Gulati et al. 1991) suggest that this effect is important in the field.

Though our understanding of food quality in zooplankton has greatly improved in recent years, one potentially important issue in food quality research that has not yet been ad-

equately addressed is temporal and spatial heterogeneity. Temporal variation over time scales of hours to days in the chemical content of algal food available to individual grazing herbivores may be driven by a variety of factors. Among these are changes in algal species composition due to population growth and loss processes and physiological changes caused by diurnal patterns of illumination and carbon fixation. Coupled to this variability is the variability induced by the vertical movements of the grazers, which would take them through horizontal strata with differing nutritive qualities.

Resource-determined growth in a variable environment has been examined from a variety of perspectives. Litchman (1997, 2000), who worked with phytoplankton in fluctuating light regimes, suggested a useful distinction. She contrasted long-term growth equal to that predicted from average resource level (i.e., long-term growth under fluctuations equals that predicted from the average light level) and long-term growth equal to that predicted from the average growth expected from the two resource states (i.e., find the two growth rates associated with high and low resources and take a weighted average of those growth rates). With nonlinear growth curves, these two long-term growth rates are not equal. She referred to the former case as “integration of irradiances” and the latter as “integration of growth rates.” Our focus is on whether animals integrate their resources, so we will refer only to the former as “integration.” Other, more theoretical, ideas about growth under resource fluctuations include the idea that variance of a resource can itself act as a resource (Levins 1979).

A fundamental question now needing attention is “How does temporal variability in food quality affect the growth of a grazing animal?” One aspect of this question concerns how much a grazing animal is able to integrate across patch types. By integration we mean carrying positive benefits from one environment into another, such that instantaneous growth may not always be predictable from knowledge of food quality in the current environment alone.

**Theoretical expectations**—One can imagine two extreme scenarios. The first is a completely nonintegrating mode, where the long-term production and growth of an animal equals the weighted sum of the expected instantaneous growth rates for each quality of food experienced over time. If there are two qualities of food experienced during some diurnal cycle, this nonintegrative mode predicts a long-term growth rate  $\mu$  from the linear combination of growth rates expected for each food type:

$$\mu = (1 - F) \times \mu_{\text{low}} + F\mu_{\text{high}}, \quad (1)$$

where  $F$  = the fraction of the day spent in high-quality food,  $\mu_{\text{low}}$  = the long-term growth rate on low-quality food alone, and  $\mu_{\text{high}}$  = the long-term growth rate on high-quality food alone. This nonintegrative mode predicts the long-term growth would be a linear function of duration in high-quality food ( $F$ ) no matter what the values of  $\mu_{\text{low}}$  and  $\mu_{\text{high}}$ .

In contrast, there may be integration of resources. In the extreme example, long-term growth over two alternating food regimes would be identical to the growth that the animal would achieve if those two foods were mixed in proportions equal to the fraction of time spent in each food per day. Evaluating integration requires knowing what kind of growth patterns to expect on food mixtures. For convenience, we will refer to the shape of these curves (growth vs. food quality) with reference to the well-known type I, II, and III functional responses of Holling (1959). A type I curve is linear over at least part of its range, a type II curve is a saturating function, and a type III curve is an S-shaped curve. Empirical studies closely resembling type II curves have been reported (Sommer 1992; Sterner 1993). A saturating curve is also seen when one plots *Daphnia* growth against P content in the work reported by DeMott (1998). For generality, we will refer to this integrative mode as

$$\mu = \mu_F, \quad (2)$$

where  $\mu_F$  equals the growth rate that animals achieve on mixed foods with fraction high-quality food equal to  $F$ ; here,  $\mu_F$  is a function of  $F$ .

A way to visualize the differences between models (1) and (2) is to consider what to expect for instantaneous growth rates under a fluctuating food regime. If an animal alternates between two foods (one associated with growth  $\mu_{\text{high}}$  and one associated with  $\mu_{\text{low}}$ ), model 1 would result from instantaneous shifts between the two growth rates as the animal moves between the two environments (Fig. 1A, line segments). In contrast, integration as defined here would result from real-time lags in response of growth to alternating food. In particular, if shifts in growth associated with movement into patches of high quality occur more rapidly than shifts in growth associated with movement into patches of low quality (Fig. 1A, smooth curves), the long-term average growth rate would be greater than expected by a nonintegrative model.

Assume a saturating (type II) curve for animal growth against food quality. In this case, when an animal spends 100% of its day in a given food type (Fig. 1B), there are clear cut expectations for growth in alternating food types in both nonintegrating and integrating modes. Growth rates 1–5 in Fig. 1C correspond to rates 1–5 where  $F = 1$  in Fig. 1B, i.e., these are both equal to 100% of the day in a single food type. When foods alternate between high and low quality, the nonintegrative mode (Eq. 1) predicts a family of lines (labeled “no storage,” Fig. 1C) extending from growth rate  $\mu_{\text{low}}$  to particular values of  $\mu_{\text{high}}$  corresponding to that particular type of high-quality food. As Eq. 1 states, all such nonintegrative modes are linear with  $F$ . In contrast, integrative growth (e.g., Eq. 2) predicts that growth rates under alternating food types ( $0 < F < 1$ ) will exceed rates predicted

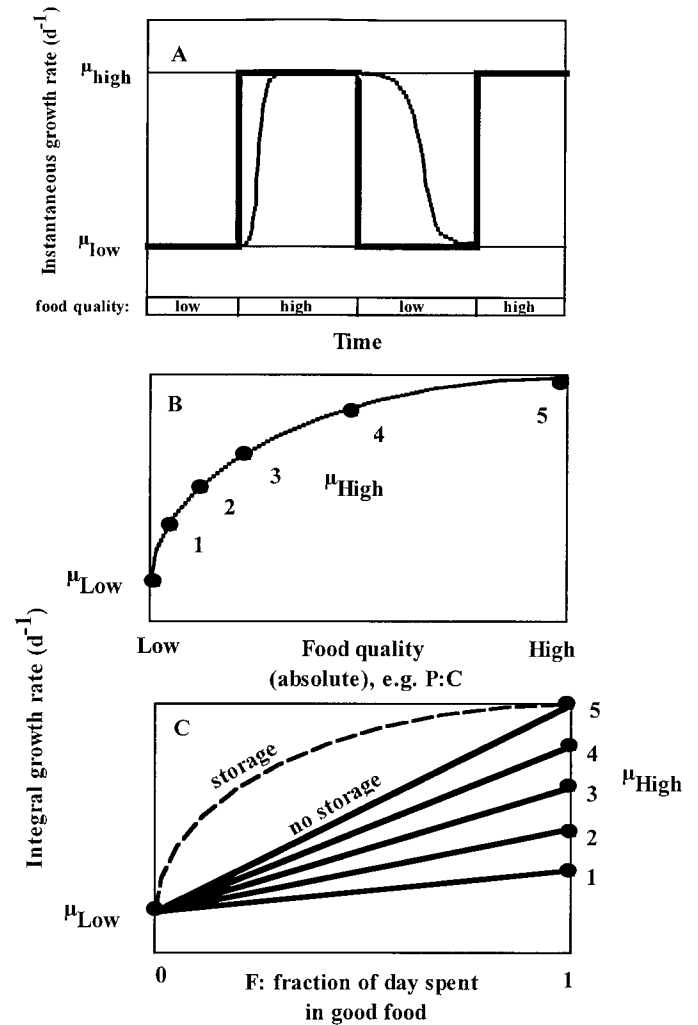


Fig. 1. Schematics showing null models for expected growth under different temporal integrative patterns. (A) Instantaneous growth versus time, with periods of feeding on high- and low-quality food indicated at the bottom. The line-segment function represents no carryover from one food type to another; the animal grows at the instantaneous rate for the conditions it is in at the moment. The smooth curves indicate carryover effects, in this case, with a more rapid adjustment to higher growth rates than down to lower growth rates. (B) Model for growth when spending 24 h per day in a single food type. (C) Model for growth when alternating between two food types (low and high quality). The dashed curve marked “storage” refers to growth alternating between low-quality and high-quality type 5 in Fig. 1B. In (B) and (C), the vertical axes represent rates observed over units of integer days, i.e., they reflect the entire daily growth increment.

under nonintegrative growth. Thus, some sort of curvilinear relationship between observed growth and  $F$  spent in good food is predicted. This integrative growth curve would be bounded at the bottom by the nonintegrative linear model (Eq. 1) and above by rates corresponding to complete integration (Eq. 2). Integrative growth is an indication that the animal has the ability to use a previously assimilated resource for growth at times of scarcity.

Table 1. Treatments used in each run. Runs 1–4 consisted of alternating food types and treatments are identified by the hours (per 24) spent in high quality food. Runs 5 and 6 were performed with animals that spent 100% of their time in mixtures of food of low and high quality. For these, treatments are given as percent of total mixture (from 0 to 100) comprised by high quality food.

Run #	Hours in high-quality food	Run #	Percent of high quality food
1	0, 5, 19, 24	5	0, 13, 21, 29, 100
2	1, 3, 7, 24	6	0, 13, 25, 50, 100
3	0, 1, 3, 5, 19, 24		
4	0, 7, 12, 15, 24		

*Laboratory experiments*—We examined the ability of grazing *Daphnia* to integrate high- and low-quality foods over time periods of 1 d by experimentally moving them between high- and low-P algal foods, adjusting the duration of the day spent in each food type. Juvenile growth rates as measured here generally correspond with more extensive demographic analysis (Lampert and Trubetskova 1996), although life history responses of *Daphnia* to low-P food also include changes in egg size and egg survival rate (Urabe and Sterner in press). For comparison, we performed similar experiments with mixed foods to see what kind of integrative model is most appropriate for those conditions.

Each run began by placing monoclonal, gravid *Daphnia magna* into 1.2-liter roller bottles that contained either 250  $\mu\text{g C L}^{-1}$  of low-quality (high C:P) *Scenedesmus acutus* or 250  $\mu\text{g C L}^{-1}$  of high-quality (low C:P) *S. acutus*. The <1-d old neonates were collected and distributed as follows. Five neonates from each bottle were measured with an eyepiece micrometer and dried at 60°C. Dry masses were recorded the next day with a Mettler microbalance ( $\pm 0.1 \mu\text{g}$ ). The remaining neonates were distributed among the different treatments in each run. Table 1 lists the treatments used in each run. The neonates that hatched in the low-quality algae were used for the treatment with no exposure to high-quality food (i.e., zero hours in high-quality food). All other treatments were begun with neonates that hatched in bottles containing high-quality algae. Two bottles per treatment were established in each run. Each of the two roller bottles contained 1.2 liters of basal COMBO medium (Kilham 1998) (i.e., lacking N and P) and 250  $\mu\text{g C L}^{-1}$  of *S. acutus*. To maintain the algae in suspension, the bottles were placed on a roller rack during the entire incubation period. The bottles were incubated at 14°C and constant light (200  $\mu\text{Ein m}^{-2} \text{s}^{-1}$ ). Following incubation in high-quality algae, each daphnid was pipetted into a “rinse” beaker containing only basal COMBO medium to remove excess algae. The daphnids were then transferred into a roller bottle containing low-quality algae for the remaining incubation length. This transfer procedure was repeated daily for 6 d, rinsing between every transfer. Treatments with the same algal quality for the entire 24 h period (i.e., zero and 24 h spent in high-quality food) were also rinsed and transferred twice a day in order to standardize handling of the animals. Variation in the number of available neonates as well as in the number of treatments within a run resulted in daphnid densities ranging between

Table 2. Neonate masses ( $\mu\text{g}$ , mean  $\pm$  SD) for each experimental run. Statistically homogeneous groups (LSD, 95% confidence level) are indicated by vertical lines.

Run	Initial animal density (mean number per bottle)	Neonate mass	
		Low P	High P
4	4.7	3.45 $\pm$ 1.28	3.27 $\pm$ 1.24
1	7.9	6.17 $\pm$ 1.00	7.54 $\pm$ 1.06
6	5.2	6.32 $\pm$ 1.31	5.35 $\pm$ 1.42
3	4.8	6.36 $\pm$ 1.31	6.46 $\pm$ 1.15
5	5.0	6.46 $\pm$ 1.16	6.61 $\pm$ 1.29
2	5.7	8.67 $\pm$ 1.60	7.17 $\pm$ 1.01

2.5 and 15  $\text{L}^{-1}$  (Table 1). Each run lasted 6 d and the experimental times used in each run differed slightly in order to test as many different time scales as possible.

Upon completion of each run, daphnids were removed from roller bottles and dried overnight at 60°C. Growth was calculated as

$$g = \ln(\text{mass}_{\text{final}} - \text{mass}_{\text{initial}})/\text{time}, \quad (3)$$

where time was in days.

Neonate mass differed across runs, but as would be expected not across food types experienced by mothers (two-way ANOVA,  $p < 0.001$ ) (Table 2). This difference, along with a difference in the number of animals per bottle (Table 2), and some likely variation in the chemical content of algae during different runs, resulted in different observed growth rates among the different runs. For this reason, statistical analysis of each run was performed separately. Bottle means were used to avoid potential pseudoreplication. Maximal growth rates were lower than observed by others (DeMott et al. 1998; Sterner and Robinson 1994) due to the fact that food concentrations were kept low in order to maintain partial food quantity limitation and high feeding rates.

Visual inspection of *D. magna* growth plotted as a function of the percent high-quality food (percent of time in alternating regimes, percent of mixture in others) strongly suggested that responses were nonlinear (Fig. 2). To test statistically whether the nonintegrative model (Eq. 1) sufficiently described the data, we first performed linear regressions followed by goodness of fit tests. In goodness of fit tests, a significant  $p$  value (small) indicates an underlying model that does not fit the data. For all six experimental runs, the lack of fit test for the linear model indicated that a linear model did not adequately describe the data ( $p < 0.001$ ). We then performed forward stepwise regression ( $p$  to enter =  $p$  to remove = 0.05) on the polynomial model:

$$g = \beta_0 + \beta_1 F + \beta_2 F^{1/2}. \quad (4)$$

Another test for curvilinearity is whether the final chosen model includes the  $F^{1/2}$  term. For five of six experimental runs this term was included in the final model (Table 3). Lack of fit tests on the final chosen polynomial models returned a marginally significant  $p$  value in run 6, but the polynomial regression adequately described runs 1–5. We do not know if the very small decreases in growth at high  $F$

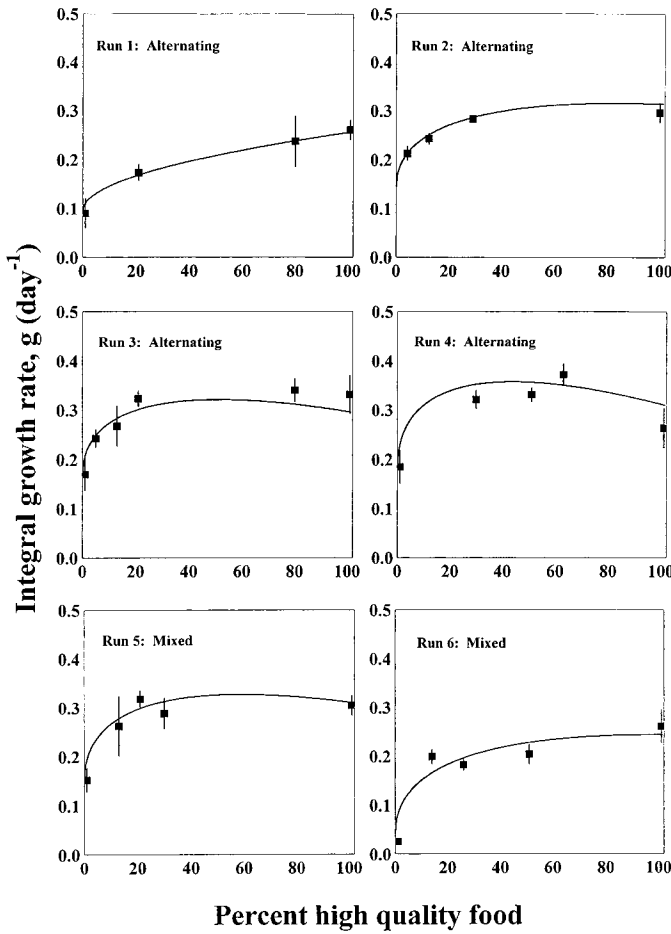


Fig. 2. *Daphnia magna* growth as a function of percent high-quality food (means  $\pm$  2 SE). Runs 1–4 were performed with alternating food types, and the horizontal axis represents the percent of 24 h the animals spent in high-quality food. Runs 5 and 6 were performed with food mixtures, and the horizontal axis represents the percent of total food made up by high-quality algae. Curves are polynomial regression model fits with coefficients and statistics described in Table 4.

for some polynomial fits are meaningful, and we will not interpret them further.

We then fit the results to a nonlinear model, similar to a Michaelis-Menten equation with an intercept:

$$g = \mu_1 + \mu_2 \left( \frac{F_{10}}{K + F} \right) \quad (5)$$

where  $\mu_1$  is the growth rate on the lowest quality food,  $\mu_1 + \mu_2$  is the asymptotic highest growth achieved on high-quality food, and  $K$  is a half-saturation constant associated with the bend in the function. Analysis of all but one run (4) yielded plausible statistical models (Table 4). For run 4, the nonlinear regression returned a negative value for  $K$  even when we tried different starting values and different options for curve fitting. The data for this run had the least apparent effect of  $F$ , fraction of high-quality food, on growth. For the other five runs, the parameter  $\mu_1$  is an estimate of growth on low-quality food. As discussed above, there are a number

Table 3. Coefficients for polynomial models ( $g = \beta_0 + \beta_1 F + \beta_2 F^{1/2}$ ) chosen using stepwise variable selection.

Run		Coefficient	$N$	$R^2_{\text{adj}}$	$p$ , Lack of fit
1	$\beta_0$	0.082	8	0.95	0.84
	$\beta_1$	—			
	$\beta_2$	0.183			
2	$\beta_0$	0.26	7		0.071
	$\beta_1$	—			
	$\beta_2$	—			
3	$\beta_0$	0.167	12	0.74	0.92
	$\beta_1$	−0.276			
	$\beta_2$	0.439			
4	$\beta_0$	0.181	10	0.82	0.11
	$\beta_1$	−0.433			
	$\beta_2$	0.530			
5	$\beta_0$	0.152	7	0.54	0.81
	$\beta_1$	−0.312			
	$\beta_2$	0.464			
6	$\beta_0$	0.044	8	0.77	0.05
	$\beta_1$	−0.205			
	$\beta_2$	0.402			

of reasons why this rate may have differed among runs in this study. These five experimental runs exhibited a pattern of growth rate response to  $F$  with an initial increase, leveling off to a plateau.

The parameter  $K$  is of particular interest. For runs with alternating food regimes, this parameter can be interpreted as the fraction of the day *Daphnia* must spend in high-quality food to achieve a growth rate reduction of 50% compared to continuous time in high-quality food. Likewise, if the animal spent  $2K$  fraction of time in high-quality food, it would achieve a growth rate equal to  $2/3$  of maximal, and if it spent  $3K$  in high-quality food, it would achieve  $3/4$  of maximal. The three values of  $K$  we observed in alternating foods were all less than 0.4, and two were less than 0.1. These statistical models suggest that *D. magna* can achieve close to maximal growth even when only spending half of the day in high-quality food. Visual inspection of the data (Fig. 2) suggests the same thing: animals achieve near maximal growth when spending half or less of their time in high-quality food.

In theory, a comparison between growth responses on alternating foods and food mixtures should be able to deter-

Table 4. Coefficients for nonlinear growth model (Eq. 6). The half-saturation constant  $K$  is dimensionless; it is the fraction of the total food or total time that is high quality ( $0 < K < 1$ ). Run 4 produced an implausible statistical model.

Run	Coefficient			Model $r^2$	$n$
	$\mu_1$	$\mu_2$	$K$		
Alternating foods					
1	0.07	0.24	0.32	0.96	8
2	0.12	0.16	0.026	0.53	7
3	0.17	0.18	0.062	0.77	12
1–4	0.14	0.16	0.044	0.88	37
Food mixtures					
5	0.15	0.17	0.038	0.71	10
6	0.14	0.16	0.035	0.55	37

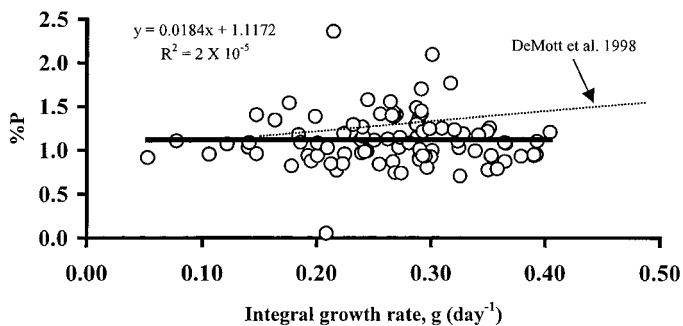


Fig. 3. P content (percent of dry mass) in individual subadult *D. magna* plotted versus observed growth rate. The dark line indicates the least-squares best-fit line (slope not statistically different from zero) with equation presented on the figure. The thinner, dotted line represents the relationship between growth and P demonstrated by DeMott et al. (1998).

mine how closely the animals came to maximal possible integration over time of the alternating resources. Under complete integration, there would be no difference between the two. Unfortunately, our data do not resolve either of these curves well enough for the comparison to be very helpful.

*Relation to the real world*—There is a wealth of information regarding the responses of various consumers to foods of differing qualities. Well-studied groups include insects (Slansky and Rodriguez 1987) and certain mammals (Moen et al. 1997), as well as crustacean zooplankton (Gulati and DeMott 1997; Sterner and Schulz 1998). However, few feeding or growth studies have considered temporal variation in food chemical content. Experiments with constant food can reveal a great deal of important information about consumer-resource interactions, but studies must also assess the couplings of environmental variation to food quality and animal growth response.

Many lakes have midsummer mixed layers with seston of low nutrient content relative to generalist herbivore demands (Elser and Hassett 1994; Hassett et al. 1997). These “high C:P” lakes seem to result from high light supply relative to phosphorus loading (Sterner et al. 1997), and experiments have shown that herbivores with high P demands can be negatively affected by increases in light, causing elevated C:P ratios in algae or seston (Urabe and Sterner 1996; Sterner et al. 1998). The role of vertical gradients in food quantity and especially quality is still very poorly understood but have been mentioned as an important priority for further research (Williamson et al. 1996). Phosphorus supply from sediments is likely to cause an overall increase in P availability with increasing depth (e.g., Elser and George 1993). Hence, migrating animals may often be exposed to an enhanced P supply when they migrate into deep layers. Although examination of vertical migration often considers deeper layers to be nutritionally inferior to surface layers, there is a dearth of empirical study of the nutritional quality of food in different layers in lakes. We might expect a common pattern to be a diel migration between layers with high and low algal P content, as simulated here. It should also be noted that our

Table 5. Mean and median P content (percent of dry mass) measured from individual animals. The difference between subadults and neonates is significant ( $p < 0.05$ ,  $t$ -test).

	Percent P		
	Mean	Median	N
Subadults	1.12	1.09	92
Neonates	1.45	1.16	30

experiment did not incorporate a change in temperature that would ordinarily be a part of migration through a thermocline. Whether our results would differ in an experiment including temperature changes is not known, but seems likely.

There is a host of potentially interesting time scales of variability in food chemical content. We expect that rapid switching back and forth between foods (on time scales less than gut passage time, i.e.,  $<1$  h) should be very similar to a mixture model (e.g., Eq. 2). On the other hand, very long time scale changes (e.g., seasonal changes) should be close to the linear model we presented earlier (Eq. 1). Daily rhythms fall on intermediate scales of fluctuations where it is difficult if not impossible to predict the degree of integration in the absence of empirical measurement. Our results suggest that resource integration over this time scale may be ecologically significant.

*P contents of individual daphnids*—Our results suggest that *Daphnia* exhibit luxury uptake of phosphorus. “Luxury uptake” is a term used to describe acquisition or assimilation of a nutrient in excess of current demands (Elrifi and Turpin 1985), and to our knowledge it is a term so far only applied to phytoplankton. Luxury uptake is a form of nutrient storage. Stored nutrients are available for growth a finite time later than those nutrients were acquired. Luxury uptake could be a means for integrating a temporally varying resource, achieving higher long-term growth rates than would be possible in the absence of storage. However, we did not directly observe changes in P content in *Daphnia* in this study; our logic for concluding that there is luxury uptake of P is therefore indirect. However, we think it is persuasive. *Daphnia* are directly P limited on low-P food under conditions such as these (Urabe et al. 1997). Growth rates at intermediate times spent in high-quality food were larger than expected from a nonintegrative model, which indicates some growth benefit occurs beyond the length of time in high-quality food. Hence, there is a very strong suggestion of some integration of the nutritional resource base. Our results imply that P assimilated during exposure to high-P food can be used subsequently when the animal is exposed to low-P food. Phosphorus storage and the so-called strict homeostasis model (Sterner 1990) are strictly incompatible. The exact degree to which P may be stored and how strict or loose homeostasis is in these animals still must be determined. However, from a broad perspective, a homeostatic model may be a useful approximation: P content of grazers is much less variable than in their food.

By measuring P content of individual animals at the end of the experiment, we attempted to confirm the results of DeMott et al. (1998), who found a positive, linear relation-

ship between *D. magna* P content and animal growth rate. P content of individual animals from neonates collected for initial samples as well as subadults from the end of the experiment was then measured using the hydrolysis, acid-molybdate method of DeMott et al. (1998). DeMott et al. measured P in groups of animals, whereas we measured it in individuals. Unfortunately, our results neither support nor reject a relationship such as they found. The measured variation in P content in individual animals in our data, where there was a greater noise to signal ratio than in larger samples of grouped animals, overwhelmed our ability to detect a trend of the magnitude reported by DeMott et al. (Fig. 3). In comparing P content in subadults and neonates, we found, as have others, that P content (percent of dry mass) decreases with maturation (Table 5). Our measured mean P content for subadult *D. magna* of 1.1% is very similar to the value for this species reported by DeMott (1998) (1.01%) but somewhat lower than the report of Vrede et al. (1999) (1.48%).

*Significance*—Having now observed integration of resources in zooplankton grazers, a series of new questions is opened. For example, in what chemical form is P stored? Where is it stored? How does it relate to the entire P budget? Are some species better able to exploit temporal variation due to enhanced storage capabilities? And, perhaps most fundamentally, how should we relate growth studies on simplified, constant foods to in situ conditions where these parameters vary in time and space?

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## References

- BRETT, M. 1993. Comment on "Possibility of N or P limitation for planktonic cladocerans: An experimental test" (Urabe and Watanabe) and "Nutrient element limitation of zooplankton production" (Hessen). *Limnol. Oceanogr.* **38**: 1333–1337.
- DEMOTT, W. R. 1998. Utilization of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by daphnids. *Ecology* **79**: 2463–2481.
- , AND R. D. GULATI. 1999. Phosphorus limitation in *Daphnia*: Evidence from a long term study of three hypoeutrophic Dutch lakes. *Limnol. Oceanogr.* **44**: 1557–1564.
- , AND K. SIEWETSEN. 1998. Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnol. Oceanogr.* **43**: 1147–1161.
- ELRIFI, I. R., AND D. H. TURPIN. 1985. Steady-state luxury consumption and the concept of optimum nutrient ratios: A study with phosphate and nitrate limited *Selenastrum minutum* (Chlorophyta). *J. Phycol.* **21**: 592–602.
- ELSER, J. J., AND N. B. GEORGE. 1993. The stoichiometry of N and P in the pelagic zone of Castle Lake, California. *J. Plankton Res.* **15**: 977–992.
- , AND R. P. HASSETT. 1994. A stoichiometric analysis of the zooplankton-phytoplankton interaction in marine and freshwater ecosystems. *Nature* **370**: 211–213.
- GULATI, R. D., AND W. R. DEMOTT. 1997. The role of food quality for zooplankton: Remarks on the state-of-the-art, perspectives and priorities. *Freshw. Biol.* **38**: 753–768.
- , K. SIEWETSEN, AND L. VAN LIERE. 1991. Carbon and phosphorus relationships of zooplankton and its seston food in Loosdrecht lakes. *Mem. Ist. Ital. Idrobiol.* **48**: 279–298.
- HASSETT, R. P., B. CARDINALE, L. B. STABLER, AND J. J. ELSER. 1997. Ecological stoichiometry of N and P in pelagic ecosystems: Comparison of lakes and oceans with emphasis on the zooplankton-phytoplankton interaction. *Limnol. Oceanogr.* **42**: 648–662.
- HESSEN, D. O. 1992. Nutrient element limitation of zooplankton production. *Am. Nat.* **140**: 799–814.
- HOLLING, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**: 385–398.
- KILHAM, S. S., D. A. KREEGER, S. G. LYNN, C. E. GOULDEN, AND L. HERRERA. 1998. COMBO: A defined freshwater culture medium for algae and zooplankton. *Hydrobiologia* **377**: 147–159.
- LAMPERT, W., AND I. TRUBETSKOVA. 1996. Juvenile growth rate as a measure of fitness in *Daphnia*. *Funct. Ecol.* **10**: 631–635.
- LEVINS, R. 1979. Coexistence in a variable environment. *Am. Nat.* **114**: 765–783.
- LITCHMAN, E. 1997. Competition and coexistence of phytoplankton under fluctuating light. Ph.D. thesis, Univ. Minnesota.
- . 2000. Growth rates of phytoplankton under fluctuating light. *Freshw. Biol.* **44**: 223–236.
- MOEN, R., J. PASTOR, AND Y. COHEN. 1997. A spatially explicit model of moose foraging and energetics. *Ecology* **78**: 505–521.
- MÜLLER-NAVARRA, D. 1995. Biochemical versus mineral limitation in *Daphnia*. *Limnol. Oceanogr.* **40**: 1209–1214.
- PATALAS, K. 1990. Patterns in zooplankton distribution and their causes in North American Great Lakes, p. 440–458. *In* M. M. Tilzer and C. Serruya, [eds.], *Large lakes*. Springer-Verlag.
- SIERSZEN, M. E., AND T. M. FROST. 1990. Effects of an experimental lake acidification on zooplankton feeding rates and selectivity. *Can. J. Fish. Aquat. Sci.* **47**: 772–779.
- SLANSKY, F., JR., AND J. G. RODRIGUEZ. 1987. Nutritional ecology of insects, mites, spiders, and related invertebrates: An overview, p. 1–69. *In* F. Slansky, Jr. and J. G. Rodriguez [eds.], *Nutritional ecology of insects, mites, spiders, and related invertebrates: An overview*. Wiley.
- SOMMER, U. 1992. Phosphorus-limited *Daphnia*: Intraspecific facilitation instead of competition. *Limnol. Oceanogr.* **37**: 966–973.
- STERNER, R. W. 1990. The ratio of nitrogen to phosphorus resupplied by herbivores: Zooplankton and the algal competitive arena. *Am. Nat.* **136**: 209–229.
- . 1993. *Daphnia* growth on varying quality of *Scenedesmus*: Mineral limitation of zooplankton. *Ecology* **74**: 2351–2360.
- , J. CLASEN, W. LAMPERT, AND T. WEISSE. 1998. Carbon: phosphorus stoichiometry and food chain production. *Ecol. Lett.* **1**: 146–150.
- , J. J. ELSER, E. J. FEE, S. J. GUILDFORD, AND T. H. CHRZANOWSKI. 1997. The light: nutrient ratio in lakes: The balance

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- of energy and materials affects ecosystem structure and process. *Am. Nat.* **150**: 663–684.
- , AND D. O. HESSEN. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu. Rev. Ecol. Syst.* **25**: 1–29.
- , AND J. ROBINSON. 1994. Thresholds for growth in *Daphnia magna* with high and low phosphorus diets. *Limnol. Oceanogr.* **39**: 1229–1233.
- , AND K. L. SCHULZ. 1998. Zooplankton nutrition: Recent progress and a reality check. *Aquat. Ecol.* **32**: 261–279.
- STIBOR, H. 1992. Predator induced life-history shifts in a freshwater cladoceran. *Oecologia* **92**: 162–165.
- TESSIER, A. J., AND R. J. HORWITZ. 1990. Influence of water chemistry on size structure of zooplankton assemblages. *Can. J. Fish. Aquat. Sci.* **47**: 1937–1943.
- URABE, J., J. CLASEN, AND R. W. STERNER. 1997. Phosphorus-limitation of *Daphnia* growth: Is it real? *Limnol. Oceanogr.* **42**: 1436–1443.
- , AND R. W. STERNER. 1996. Regulation of herbivore growth by the balance of light and nutrients. *Proc. Natl. Acad. Sci. USA* **93**: 8465–8469.
- , AND ———. In press. Contrasting effects of different types of resource depletion on life history traits in *Daphnia*. *Funct. Ecol.*
- VREDE, T., T. ANDERSEN, AND D. O. HESSEN. 1999. Phosphorus distribution in three crustacean zooplankton species. *Limnol. Oceanogr.* **44**: 225–229.
- WILLIAMSON, C. E., R. W. SANDERS, R. E. MOELLER, AND P. L. STUTZMAN. 1996. Utilization of subsurface food resources for zooplankton reproduction: Implications for diel vertical migration theory. *Limnol. Oceanogr.* **41**: 224–233.

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## In situ exposure to ultraviolet radiation alters the depth distribution of *Daphnia*

**Abstract**—Damaging solar radiation was one of the first factors proposed to explain zooplankton diel vertical migrations (DVM), yet other factors such as temperature, food, and especially predation have typically been more widely studied and identified as the primary factors inducing DVM. This is true in spite of the fact that recent experiments have shown that ambient levels of solar ultraviolet radiation (UVR) are potentially lethal to zooplankton and negative phototactic behavior has been demonstrated in the laboratory. Here we present the first evidence from in situ experiments demonstrating that UVR wavelengths influence the vertical swimming behavior of zooplankton under full spectrum solar radiation. Cylindrical acrylic columns that transmitted or blocked UVR were used to examine the behavioral responses of *Daphnia pulex* to UVR. Experiments were conducted in the epilimnion of a high-UV system at midday and in late afternoon. In both experiments, a large proportion of individuals migrated downward in the presence of UVR, whereas those in the UVR-shielded treatments tended to remain closer to the surface.

The water column of lakes and oceans can be thought of as a vertical habitat gradient that varies in many abiotic and biotic factors including temperature, light, food, and predation. Although all of these factors contribute to the vertical distribution of organisms, migrations that involve daily changes in vertical distribution are generally connected with factors that vary on a diel basis, such as light and predation. Some of the earliest works on diel vertical migration (DVM) demonstrated that sunlight was a potential proximate as well as ultimate factor inducing migrations. Both negative phototactic behavior (Moore 1912) and increased mortality rates were observed in freshwater and marine organisms exposed to ultraviolet radiation (UVR) (Huntsman 1924; Klugh 1930).

In spite of this evidence for the potential importance of

sunlight in small-scale experimental studies, no field studies were conducted to demonstrate a clear link between damaging solar radiation and zooplankton migration patterns in nature. In addition, although most investigators agree that multiple factors are important in inducing DVM, damaging light has been given little attention in comparison to other factors, such as temperature, food availability, and especially predation (Haney 1988; Kerfoot 1985; Lampert 1989).

Both intensity and spectral composition of light have been shown to be important in the vertical migration and associated behavioral responses of zooplankton. For example, a strong relationship has been demonstrated between lake transparency and the magnitude of *Daphnia* vertical migrations in nature (Dodson 1990). Laboratory experiments with polychromatic light have demonstrated that cladocerans are negatively phototactic to short-wavelength blue light but positively phototactic to long-wavelength red light (Smith and Baylor 1953). These “color dances” were hypothesized to cue zooplankton to high concentrations of algal food but were also thought to influence DVM. More recent studies with monochromatic light have demonstrated that *Daphnia magna* are positively phototactic to visible light (420–600 nm) and negatively phototactic to UVR (260–380 nm) with maximal sensitivity at 340 nm (Storz and Paul 1998). In addition to these laboratory experiments, field studies have shown that just a few days exposure to natural levels of solar UVR in the surface waters of lakes can be lethal to zooplankton (Williamson et al. 1994).

The combined results of these studies strongly suggest the potential role of damaging solar UVR in influencing diel vertical migration behavior in UVR sensitive organisms; however, no studies have directly examined the role of UVR as a proximate factor of DVM in the presence of full spectrum solar radiation. The contrasting responses of *Daphnia*