

# Foraging behavior by *Daphnia* in stoichiometric gradients of food quality

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**Abstract** Mismatches in the elemental composition of herbivores and their resources can impact herbivore growth and reproduction. In aquatic systems, the ratio of elements, such as C, P, and N, is used to characterize the food quality of algal prey. For example, large increases in the C:P ratio of edible algae can decrease rates of growth and reproduction in *Daphnia*. Current theory emphasizes that *Daphnia* utilize only assimilation and respiration processes to maintain an optimal elemental composition, yet studies of terrestrial herbivores implicate behavioral processes in coping with local variation in food quality. We tested the ability of juvenile and adult *Daphnia* to locate regions of high-quality food within a spatial gradient of algal prey differing in C:P ratio, while holding food density constant over space. Both juveniles and adults demonstrated similar behavior by quickly locating (i.e., <10 min) the region of high food quality. Foraging paths were centred on regions of high food quality and these differed significantly from paths of individuals exposed to a homogeneous environment of both food density and food quality. Ingestion rate experiments on algal prey of differing stoichiometric ratio

show that individuals can adjust their intake rate over fast behavioral time-scales, and we use these data to examine how individuals choose foraging locations when presented with a spatial gradient that trades off food quality and food quantity. *Daphnia* reared under low food quality conditions chose to forage in regions of high food quality even though they could attain the same C ingestion rate elsewhere along a spatial gradient. We argue that these aspects of foraging behavior by *Daphnia* have important implications for how these herbivores manage their elemental composition and our understanding of the dynamics of these herbivore–plant systems in lakes and ponds where spatial variation in food quality is present.

**Keywords** Foraging behavior · Stoichiometry · Spatial gradients · Food quality · *Daphnia*

## Introduction

In both marine and freshwater systems, the ratio of key elements in algal food supplies e.g., C:P:N has been shown to be a major determinant of food quality for herbivores, such as *Daphnia* (DeMott 2003), rotifers (Rothhaupt 1995; Jensen and Verschoor 2004), and some copepods (Kiorboe 1989; Jones and Flynn 2005). A large mismatch between elemental ratios of resources and consumers can have significant effects on growth, reproduction, and mortality of consumers (Sterner and Hessen 1994). Recent reviews have highlighted the role that variation in elemental ratios can play in explaining features of both populations and communities (e.g., Andersen et al. 2004; Moe et al. 2005). There has also been extensive work on understanding how changes in key environmental factors (e.g., light and nutrient supply) create variation in elemental ratios in both

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time and space (Elser and George 1993; Kreeger et al. 1997). Experimental bioassays of growth and reproduction of herbivores in natural systems have linked these responses to temporal (Sterner and Schwalbach 2001) and spatial variability (Williamson et al. 1996) in elemental ratios, but there has been little work examining whether aquatic herbivores, such as *Daphnia*, respond behaviorally to spatial variation in the elemental composition of their food supply. Here, we test whether individual foragers can detect spatial variation in food quality and identify behavioral mechanisms used by individuals to forage in regions of high food quality.

*Daphnia* is an ideal freshwater herbivore when investigating questions about dynamics of individuals and populations. Their algal prey display wide variation in the ratio of C:P in lakes and ponds (Hecky et al. 1993; Hessen et al. 2003), and there has been extensive research documenting how *Daphnia* growth and reproduction is affected by variation in the C:P ratio of its algal food supply (Sterner 1993; Boersma et al. 2001; DeMott 2003). While *Daphnia* does not display strict homeostasis for elemental ratios of C:P (Plath and Boersma 2001; DeMott et al. 2004b), individuals do tend to maintain tissue ratios within relatively narrow bounds e.g., 80 and 125 (Hessen 1990; Plath and Boersma 2001; DeMott 2003). A key question is how individuals achieve these levels of regulation when exposed to variation in algal C:P ratios. Current models of individual growth and reproduction assume that consumers utilize aspects of assimilation and respiration to manage their element composition (Sterner 1997; Logan et al. 2004; Anderson et al. 2005; Darchambeau 2005). However, work done within terrestrial systems has demonstrated that an organism's behavior plays a role in the consumption of suitable resources (see review by Huntly 1991), and this behavior can have a strong effect on the dynamics exhibited by populations (Hassell and May 1974).

Recent models parameterized for the *Daphnia*–algal system show that incorporating stoichiometric regulation of P and C by *Daphnia* introduces new qualitative dynamical features (Andersen 1997; Andersen et al. 2004), such as novel equilibria and deterministic extinction, as well as quantitative effects on stability (Loladze et al. 2000; Muller et al. 2001; Hall 2004; Fan et al. 2005). All of these models assume well-mixed environments and no environmental heterogeneity or subdivision. Yet in natural systems, environmental gradients in light and nutrient supplies are known to create spatial gradients in food quality of algae as measured by variation in C:P ratio (Urabe and Sterner 1996; Diehl et al. 2002; Urabe et al. 2002; DeMott et al. 2004a) and the effects of these gradients on *Daphnia* production are well documented (Park et al. 2004). Previous research has demonstrated that

*Daphnia* can respond very quickly to spatial gradients in food quantity (Cuddington and McCauley 1994; Neary et al. 1994; Larsson 1997; Jensen et al. 2001). Both juveniles and adults aggregate in regions of high food quantity and shifting the location of these gradients in space evokes a corresponding change in foraging location. An open question is whether *Daphnia* respond behaviorally to gradients in food quality?

We have modified the flow-through system used by Cuddington and McCauley (1994) and Larsson (1997) to examine the behavioral response of *Daphnia* to spatial gradients in food quality (C:P ratio of algal cells). We address three major questions: (1) can *Daphnia* detect differences in food quality and if so, (2) will individuals exhibit behavior that allows them to remain in regions of high food quality, and (3) do juveniles and adults exhibit similar behavior? To answer these questions we compare the foraging paths of juvenile and adult *Daphnia* under conditions of spatially uniform food density and food quality with spatially heterogeneous food quality holding food density constant over space. *Daphnia* within the homogeneous environment are predicted to display a uniform search path within the chamber due to a uniform food environment. If individuals exposed to the food quality gradient distribute themselves within regions of high food quality, this would indicate an ability to perceive differences in food quality given that all other environmental characteristics are controlled. By following individual *Daphnia*, we can use turning frequencies to characterize behavioral responses and provide insight into how spatial variation in foraging arises in response to spatial gradients in food (Winder et al. 2004; Lampert et al. 2003; Lampert 2005).

## Materials and methods

All foraging and ingestion experiments used the green alga *Chlamydomonas reinhardtii* as the food source for *Daphnia pulex*. Algal cultures were grown in COMBO growth media (Kilham et al. 1998) with light intensity and P concentration manipulated to obtain differences in the C:P ratio of cells. Cultures were sampled for cell density, particulate C and particulate P. Cell density was determined by preservation in Lugol's solution and subsequent counting in a Sedgwick-Rafter counting slide. Particulate C was measured by filtering samples through precombusted quartz membrane filters. Filters were then combusted at 800°C and analyzed using a Dohrmann DC-180 total organic C analyzer. Particulate P was measured using the ammonium molybdate method. Prior to the foraging and ingestion experiments, replicate algal cultures were measured to demonstrate reproducibility of algal C:P ratios.

## Foraging experiments

Individual *D. pulex* movements in response to food gradients were observed in a plexiglass chamber, in the form of a torus (S1), adapted from Cuddington and McCauley (1994). The chamber has a width of 1.5 cm and a height of 5.2 cm. The circumference measured at the center of the foraging area is 56.5 cm. The trials took place within a walk-in incubator with a temperature of 19°C, and light intensity of 0.5  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ . Algal gradients were created in the chamber using flows fed by different algal reservoirs. Eleven input and output ports (yielding 11 distinct sections) were connected to peristaltic pumps with Tygon tubing (1.6 mm inside diameter). Inputs were fed from reservoirs of algae suspended in COMBO media free of N and P so as not to alter cell quality or promote growth. Based on individual clearance rates (Porter et al. 1982), flow was maintained at approximately 40 ml h<sup>-1</sup> for each channel so that an individual could not depress the density of food in a given area. As well, the flow rate should also prevent excretion products from altering local C:P of algal cells. Samples were collected for each treatment from each output channel and analyzed for cell density, particulate C, and particulate P. Analyses of the output confirmed the occurrence of food gradients in our experimental apparatus.

Five treatments were created reflecting several combinations of food quality and quantity gradients (Table 1). Prior to commencing the behavior experiment, algal cultures with appropriate C:P values were counted and diluted to the appropriate density for each treatment. Each experimental trial consisted of following one individual for 30 min with the spatial location recorded every 10 s. All trials consisted of only one individual in the chamber at a time, and the flow-through algal environment was created independently each trial. *Daphnia* for all treatments were taken from a persistent population grown under low food quality (molar C:P > 300) and just prior to the trial, each individual was allowed to forage in COMBO media without algae for 3 h to clear its gut. In Results, we present data

on two representative individuals per treatment with statistical tests including all replicate individuals.

## Data analysis of foraging behavior

The path of each individual was recorded by plotting its position on transparency film wrapped around the chamber. These films were then scanned and the positions digitized to a spreadsheet. Positions were measured by angles ranging from 0 to 6.28 rad with the starting point for each individual represented by the 0/6.28 rad boundary.

In analyzing the movement of an individual, the first 5 min were removed from each individual trial in order to remove bias due to initial acclimation. Either reducing or increasing the acclimation period by 2 min does not alter the conclusions. Given that the same gradient was experienced on either side of the starting position, spatial locations were grouped into five distinct sections based on food quality and quantity for each treatment. We tested the distributions of individuals exposed to a food quality gradient against the distribution of control individuals (spatially homogeneous density and low quality), as well as a hypothesized distribution based on the relative P content of the food, using a *G*-test for goodness of fit (Sokal and Rohlf 1995). The test utilizes the five values for frequency of occurrence (i.e., the number of times an individual is observed in each of the five C:P levels) which are averaged across individuals within each treatment. This likelihood ratio test evaluates differences between the observed and expected distribution with the expectation based on differences in C:P ratio. This approach was utilized by Larsson (1997) to test for aggregation in regions of high food quantity. The hypothesized P distribution (HPD) for our chambers was based on the relative proportion of P within each section of the chamber to the total P in the chamber. Thus, if an individual is foraging based on its intake of P, it should follow the HPD and spend the majority of its time in the low C:P (high-quality) sections. Since our null hypothesis for this comparison is the HPD, *P*-values > 0.05 indicate that individuals are foraging according to the relative P concentration within a section.

**Table 1** Conditions experienced by individual *Daphnia* during the foraging experiments

Treatment	Independent trials	Age class <sup>a</sup>	Food quality raised in	Food quantity gradient	Food quality gradient	Starting position
B1	3	Adult	Low	No	No	NA
B2	5	Adult	Low	No	Yes	Low food quality
B3	5	Juvenile	Low	No	Yes	Low food quality
B4	5	Adult	Low	No	Yes <sup>b</sup>	Low food quality
B5	3	Adult	Low	Yes	Yes	Low quality/high quantity

<sup>a</sup> Lengths for juvenile and adult *Daphnia* are 1.0 ± 0.1 mm and 2.0 ± 0.1 mm, respectively

<sup>b</sup> Torus divided into three sections (low, medium, and high C:P; see Results for ratios)

## Ingestion experiment

To test whether individuals adjust their ingestion rates as a function of food quality, we measured ingestion rates under four different algal C:P ratios (325, 298, 116, and 33) which are representative of variation found in the field and used in our foraging experiments. A volume of algal suspension was taken from each culture, centrifuged, and the cells were then resuspended in N- and P-free media to a concentration of 40,000 cells ml<sup>-1</sup>. Vials of 50 ml were used to hold the algal suspension to which the *Daphnia* were added. Six individual *D. pulex* of equal body length (2.0 ± 0.1 mm) were added to each feeding vial. These individuals were taken from populations grown on poor-quality algae at 19°C, and placed in N- and P-free COMBO media for 3 h to clear their guts. The vials were placed on a rotating plankton wheel turning at 2 r.p.m. to maintain cells in suspension and their accessibility to the *Daphnia*. The trials were performed in the dark in an incubator at 19°C. Each treatment and its control (zero *Daphnia*) consisted of 12 replicate vials. We removed three vials per treatment from the experiment at 2, 5, 10, and 20 h and preserved the algae in Lugol's solution for microscopic enumeration of cell densities (Peters 1984).

A maximum rate of ingestion ( $I_{\max}$ ) was estimated for each of the four treatments from the slope of the exponential decay function fitted to the data. The relationship between  $I_{\max}$  and algal C:P was estimated using linear regression analysis. Estimated values of  $I_{\max}$  for a given C:P ratio were used to predict an individual's position during the foraging experiment (Table 1, B5) based on its ingestion rate (mg C day<sup>-1</sup>) for a given food quality and food concentration.

It is well established that *Daphnia* possesses a type 2 functional response (e.g., Demott 1982) and we used parameter values [ $I_{\max}$  and half saturation constant ( $F_h$ )] for our clone that had been independently established and tested (Nisbet et al. 2004). The following equation estimates ingestion based on food concentration and a constant  $I_{\max}$ :

$$I = \frac{I_{\max} \times F}{F_h + F}, \quad (1)$$

where  $I$  is the ingestion rate,  $I_{\max} = 0.017$  mg C day<sup>-1</sup>,  $F$  is the algal biomass (mg C l<sup>-1</sup>), and  $F_h = 0.12$  mg C l<sup>-1</sup>. Ingestion was also calculated based on an  $I_{\max}$  that varies with algal C:P:

$$I = \frac{I_{\max}(\text{C:P}) \times F}{F_h + F}, \quad (2)$$

where  $I$  is the ingestion rate,  $I_{\max}(\text{C:P}) = f(\text{C:P})$ ,  $F$  is the algal biomass (mg C l<sup>-1</sup>), and  $F_h = 0.12$  mg C l<sup>-1</sup>.

## Results

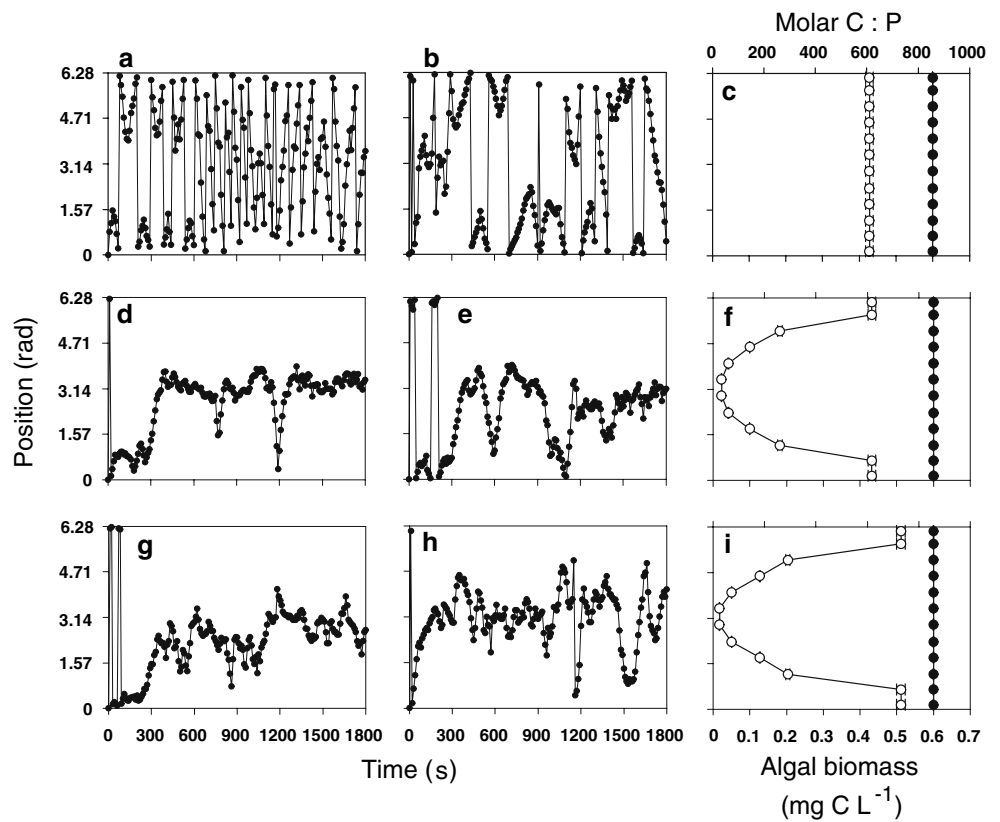
Individual *Daphnia* presented with both a homogeneous spatial distribution of food concentration and C:P ratio displayed no apparent preference for any spatial location (Fig. 1a, b). The movement path followed by adult individuals produces a distribution not significantly different from uniform (Table 2; B1). Their turning frequencies (Fig. 2a) reveal a higher proportion of turns within the starting section. However, there are no large differences between turning frequencies for the other sections of the chamber. Following the initial acclimation period, individuals proceeded to search throughout the entire chamber for the duration of the 30-min observational period.

Adults exposed to a food quality gradient with uniform cell density showed significantly different behavior (Fig. 1d, e). Individuals orient themselves around the section of higher food quality and regions directly adjacent to it. Individuals starting out in low food quality regions locate regions of high food quality very quickly (i.e., within 5–10 min of each trial). Their location may momentarily deviate from the higher quality region, but ultimately the individual returns to this region and remains there. Turning frequencies (Fig. 2b) for the adults show that a higher proportion of turns occur in the higher quality sections (i.e., spatial regions with low C:P ratios). An analysis of the frequency distributions indicates that individuals frequent the highest food quality section to an even greater extent than predicted by the relative P content of food (Table 2; B2). A comparison between individuals exposed to a homogeneous food environment and individuals exposed to a food quality gradient with uniform cell density demonstrates that individual foraging is significantly different between these two conditions ( $G=350.12$ ;  $df = 4$ ;  $P < 0.001$ ).

Juveniles presented with gradients in food quality show similar movement paths as the adults, which centred on the higher quality regions (Fig. 1g, h). In general, deviations in movement around the high food quality sections are greater for juveniles, but not significantly different from those of the adults [ $F_{0.05(4,4)} = 1.23$ ;  $P > 0.05$ ]. An analysis of the turning (Fig. 2c) and frequency distributions indicates that juveniles show a significantly different distribution from uniform (Table 2; B3), and frequent each section as predicted by the HPD (Table 2; B3).

We tested whether adult *Daphnia* could detect more discrete patches of food quality by presenting an individual with three sections in the torus (C:P ratios of 45, 220, and 475) rather than a gradient involving five sections. Five adult individuals also rapidly located the high food quality patch as in the gradient trials and demonstrated a distribution significantly different from uniform (Table 2; B4).

**Fig. 1a–i** Position (reported in radians) of individuals ( $n = 2$ ) within the observation chamber plotted as a function of time for *Daphnia*. **a, b** Adult control. **d, e** Adult treatment. **g, h** Juvenile treatment. **c, f, i** *Daphnia* food quality and density are shown as algal cellular molar C:P ( $\pm$ SE; open circles) and biomass (mg C L<sup>-1</sup>; filled circles), respectively. The SEs of biomass are smaller than the width of datapoints. Large distances between points relative to the majority indicate movement across the 0/6.28 rad boundary. Points for section 11 have been added to both the top and bottom of the plot to demonstrate the torus shape of the chamber (S1). Adult controls (**a, b**) experience homogeneous food quality and density throughout the chamber, while treatment adults (**d, e**) and juveniles (**g, h**) experience a food quality gradient (starting at lowest food quality) with uniform cell density



**Table 2** Averages within a treatment tested against a uniform distribution and hypothesized P distribution (HPD) based on the relative P content of food within a gradient. The initial 5 min have been removed from each trial to remove any bias due to acclimation

Treatment	Uniform G-value <sup>a</sup> , df = 4	P	HPD G-value <sup>a</sup> , df = 4	P
B1	1.27	>0.05	NA	NA
B2	194.51	<<1 × 10 <sup>-5</sup>	15.79	<0.005
B3	99.56	<<1 × 10 <sup>-5</sup>	1.55	>0.05
B4	25.54 (df = 2)	<1 × 10 <sup>-5</sup>	NA	NA
B5	152.13	<<1 × 10 <sup>-5</sup>	23.00	<0.005

<sup>a</sup> The G-test utilizes the five frequencies from each section and tests for deviations from a specified distribution

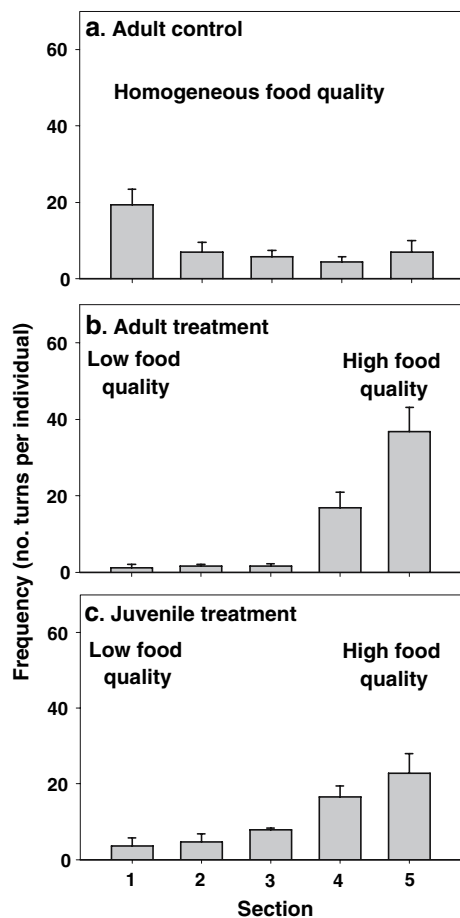
The aggregation of individual foraging trials in regions of high food quality on a relatively fast time-scale raises questions about whether individuals can alter foraging rates when exposed to differences in food quality. Experimental measurement of maximum ingestion rates using algal prey with different C:P ratios shows that adult individuals quickly increase ingestion rates with decreases in C:P ratio of the food (Fig. 3). Maximum ingestion rates (mg C day<sup>-1</sup>) decrease linearly with increasing algal C:P ratio ( $I_{\max} = 0.03956 - 0.00007685 \times \text{algal C:P}$ ;  $df = 3$ ;  $P < 0.05$ ) These rates along with functional response estimates on our *D. pulex* clone (Nisbet et al. 2004) were

used to predict expected ingestion rates for individuals experiencing a trade-off in food quality and quantity.

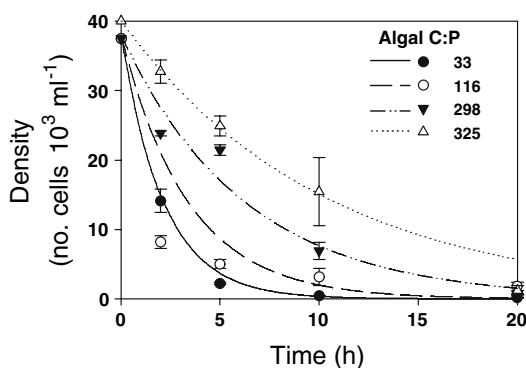
Building on the evidence for a behavioral response to changes in food quality, experiments were conducted to test *Daphnia*'s ability to detect spatial differences when food quality and food quantity co-vary inversely in space. When presented with a trade-off between food quality and concentration (Fig. 4b), that is areas of high food quality/low concentration as opposed to low quality/high concentration, individuals follow a path that is oriented around the section of high quality/low concentration (Fig. 4a). Expected ingestion rates were calculated for each section either as a function of food concentration and constant  $I_{\max}$  (Eq. 1), or as a function of food concentration and  $I_{\max}$  that varies as a function of the C:P ratio (Eq. 2; Fig. 4c). On average, individuals were found to frequent the high quality/low concentration section to an even greater extent than predicted by the HPD (Table 2; B5) as opposed to a distribution based on the concentration of cells in a given section (Fig. 5).

**Discussion**

When presented with spatial gradients in food quality, individuals rapidly located (i.e., <5–10 min) spatial regions of high food quality and altered their foraging behavior to



**Fig. 2** Average number of turns (change in swimming direction for an individual)  $\pm$ SE exhibited by **a** adult control, **b** adult treatment, and **c** juvenile treatment in one of five sections during each trial. The original 11 sections were combined to form five sections ranging from low food quality (1) to high food quality (5). There was one individual *Daphnia* per trial with five trials for each treatment (except three trials for adult control). The density of algae for all treatments was  $0.6 \text{ mg C l}^{-1}$ , distributed homogeneously throughout the chamber

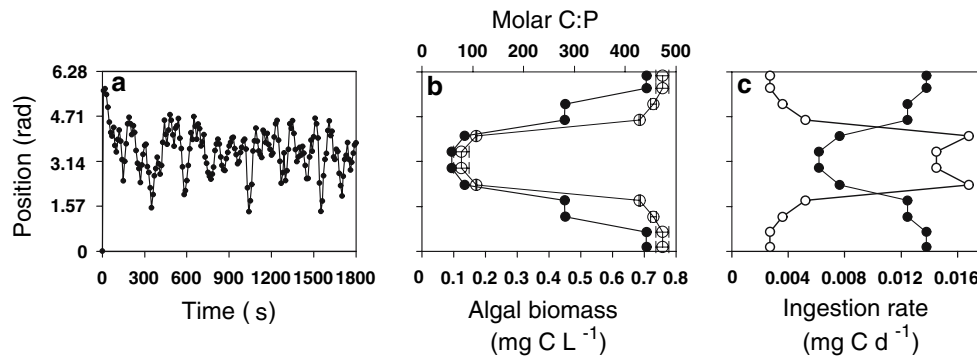


**Fig. 3** Density of *Chlamydomonas reinhardtii* cells (mean  $\pm$  95% confidence interval,  $n = 3$ ) as a function of time within feeding vials containing six 2.0-mm *Daphnia pulex* at 33 (filled circle), 116 (open circle), 298 (filled inverted triangle) and 325 (open triangle) algal C:P ratios

remain in these regions. Both juveniles and adults located the high-quality regions on approximately the same time-scale, even though swimming speeds for adults are higher than for juveniles (Ryan and Dodson 1998). In contrast, individuals exposed to a homogeneous environment of food quality and quantity foraged randomly, showing no clear preference for any region of the chamber (i.e., physical location). These individuals foraged in a manner that is significantly different from individuals found in environments with a food quality gradient. Our observations on foraging by individuals exposed to homogeneous food concentrations are consistent with previous work investigating foraging patterns that did not attempt to manipulate food quality (Jakobsen and Johnsen 1987; Neary et al. 1994; Cuddington and McCauley 1994; Larson 1997).

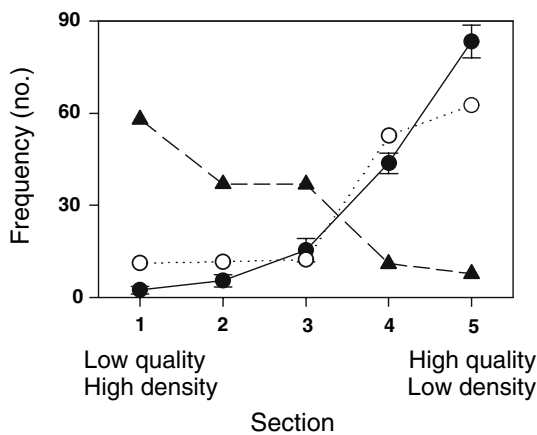
The rapid behavioral response of juveniles and adults raises important questions about mechanisms that individuals use to assess food quality of the environment relative to their own “stoichiometric state”. Our results suggest that common assumptions used to model the dynamics of consumers in the presence of variation in prey quality and quantity should be re-examined to include aspects of foraging behavior as a complement to only digestive processes. At present, models typically assume that stoichiometric regulation, or the maintenance of “elemental homeostasis”, involves only assimilatory mechanisms coupled with respiration (Sterner 1997; Logan et al. 2004; Anderson et al. 2005; Darchambeau 2005). The rapid changes in foraging observed in our study suggest that there can be a strong behavioral component in these processes. Individuals must be using a food quality “cue” that does not depend on digestion or assimilation as this would dictate response times on the order of 1–3 h (Peters 1984) rather than the 5–10 min observed here. Furthermore, our ingestion rate experiments show changes in foraging rate can operate very quickly. Our ingestion rate experiments are consistent with previous results from Sterner and Smith (1993) and Vandonk and Hessen (1993), but we must point out that Plath and Boersma (2001) and Darchambeau and Thys (2005) found that individual *Daphnia* also increased their ingestion rate when exposed to poor food quality. One explanation for the differences among ingestion studies could be accounted for by different acclimation procedures reflecting internal stimuli for foraging (e.g., Plath 1998). Experiments have shown that individuals acclimated under poor food quality conditions respond by accelerating feeding when presented with high-quality food, whereas individuals not acclimated behave differently (Plath and Boersma 2001; Darchambeau and Thys 2005).

A second key question concerning the rapid foraging response concerns what mechanisms *Daphnia* utilize to assess changes in food quality prior to digestion. It is well



**Fig. 4a–c** Response of one representative adult *Daphnia* subjected to a food quality/quantity trade-off within the observation chamber. **a** *Daphnia* position in chamber. **b** *Daphnia* food quality and density shown as algal cellular molar C:P ( $\pm$ SE; open circle) and biomass (filled circle). The SEs of biomass are smaller than the width of datapoints. **c** Predicted algal ingestion rate with constant  $I_{max}$

( $0.017 \text{ mg C day}^{-1}$ ; filled circle) and variable  $I_{max}$  ( $I_{max} = 0.03956 - 0.00007685 \times \text{algal C:P}$ ; open circle).  $I_{max}$  equals the maximum rate of ingestion ( $\text{mg C l}^{-1}$ ) for an individual given a type II functional response. Points for section 11 have been added to both the top and bottom of the plots to demonstrate the torus shape of the chamber



**Fig. 5** Average frequency of occurrence  $\pm$  SE in each of five sections (filled circle) for three *Daphnia* adults in the trade-off experiment. Sections ranged from low food quality and high density (1) to high food quality and low density (5). Hypothesized distributions for individuals choosing regions of high food quality (open circle) or regions of high food density (filled triangle) are shown. Points have been joined on each distribution for ease of comparison

known from foraging experiments involving mixtures of highly edible prey and noxious algal species (e.g., blue-green algae) that *Daphnia* can indeed reject an undesirable food bolus as it is manipulated at the mandibles (Richman and Dodson 1983; Chowfraser and Sprules 1986). In addition, a large body of evidence exists demonstrating the important role that chemical cues play in the behavioral response of *Daphnia* to such things as food and predators (see review by Larsson and Dodson 1993). But, we do not know how cell surface properties are affected by changes in the C:P ratio and how these differences in cell surface chemistry are detected by *Daphnia* (e.g., Gerritsen and Porter 1982).

Our results also raise interesting questions about how individuals forage in the presence of spatial variation in food quality in natural conditions (e.g., Rothhaupt 1991; Elser and George 1993; DeMott et al. 2004a; Park et al. 2004). Recent work has established that spatial gradients in food quality can be created via several mechanisms like changes in the environmental ratios of nutrient and light levels (Urabe and Sterner 1996; Sterner et al. 1998; Hessen et al. 2002; Hall et al. 2004), or changes in species composition through space (Rothhaupt 1991). In addition, important linkages between spatial variation of food quality and individual performance (e.g., growth and/or reproduction) of *Daphnia* have been established in both experimental and natural situations (e.g., Urabe and Sterner 1996; Williamson et al. 1996; DeMott et al. 2004a; Park et al. 2004). It remains to be tested whether variation in food quality significantly influences vertical migratory responses by *Daphnia*, but our results suggest that the time-scale for behavioral responses could play an appropriate role in vertical migratory behavior or in responses to externally imposed spatial gradients in food quality.

Extensive work has been done on optimal foraging by *Daphnia* (Johnsen and Jakobsen 1987; Plath and Boersma 2001; Kessler and Lampert 2004). Experimental evidence demonstrates that the distribution of organisms in space follows an ideal free distribution with costs (Lampert et al. 2003; Lampert 2005), which seems appropriate given that suitable habitat for *Daphnia* is determined by such things as food quantity, predators, and temperature. Individuals appear to perceive these factors and optimize fitness; however, the effect of food quality has not been considered. In our experiments, we examined only one of many possible trade-offs involving food quantity and food quality. While *Daphnia* does not strictly regulate its C:P ratio (Main et al. 1997; DeMott et al. 1998; Plath and Boersma

2001; DeMott 2003; DeMott et al. 2004b), individual *Daphnia* raised on a low food quality diet chose to forage in regions of high quality over quantity when presented with environments where ingestion rates (i.e., C consumed per unit time) were similar. Individuals could achieve the same C intake rates at any spatial location, but chose to forage in regions where P intake rates were higher relative to C intake rates. Further experiments are needed, but these experiments need to be guided by theory that uses multiple currencies to derive predictions. Dynamic energy budget models exist for the single currency case (Noonburg et al. 1998; Kooijman 2000; Nisbet et al. 2000, 2004), but are only now being parameterized for multiple currencies (Muller et al. 2001; Kooijman et al. 2004; Kuijper et al. 2004; Vrede et al. 2004).

Finally, our results suggest that population level dynamics could be significantly altered by the ability of individual foragers to rapidly assess spatial variation in food quality and modify their foraging location. Current consumer-resource models that attempt to capture food quality effects (e.g., Andersen 1997; Hessen and Bjerkeng 1997; Loladze et al. 2000; Muller et al. 2001; Andersen et al. 2004; Grover 2004; Hall 2004; Loladze et al. 2004; Fan et al. 2005) assume mass action, no behavioral aggregation, and no spatial variability either in the form of gradients or ephemeral patches [however, see Miller et al. (2004) for recent work on addition of spatial patches differing in food quality but no foraging behavior by herbivores between patches]. It is well known that aggregation by predators in regions of high prey density can dramatically alter dynamics of these systems, and extensive empirical work in terrestrial systems has demonstrated the importance of including spatial mechanisms. Perhaps new spatial models of *Daphnia* populations constrained by stoichiometric influences interacting with algal prey of varying quantity and quality could explain some well-known features of the coupled plant–herbivore systems in lakes (e.g., Lampert 1987; McCauley and Murdoch 1987, 1990; Andersen 1997; Winder et al. 2004; Lampert 2005).

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