Multiple dynamics in a single predator–prey system: experimental effects of food quality

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Recent work with the freshwater zooplankton *Daphnia* has suggested that the quality of its algal prey can have a significant effect on its demographic rates and life-history patterns. Predator–prey theory linking food quantity and food quality predicts that a single system should be able to display two distinct patterns of population dynamics. One pattern is predicted to have high herbivore and low algal biomass dynamics (high HBD), whereas the other is predicted to have low herbivore and high algal biomass dynamics (low HBD). Despite these predictions and the stoichiometric evidence that many phytoplankton communities may have poor access to food of quality, there have been few tests of whether a dynamic predator–prey system can display both of these distinct patterns. Here we report, to the authors' knowledge, the first evidence for two dynamical patterns, as predicted by theory, in a single predator–prey system. We show that the high HBD is a result of food quantity effects and that the low HBD is a result of food quality effects, which are maintained by phosphorus limitation in the predator. These results provide an important link between the known effects of nutrient limitation in herbivores and the significance of prey quality in predator–prey population dynamics in natural zooplankton communities.

Keywords: predator–prey; multiple dynamics; food quality; population dynamics; *Daphnia pulex*

1. INTRODUCTION

Herbivores face considerable challenges in obtaining the essential elements for growth (such as carbon, nitrogen and phosphorus) while feeding on prey resources that vary widely in their concentrations of these elements. Because of the large variation in prey stoichiometry (Hessen & Andersen 1992; Elser & Urabe 1999), herbivores in both terrestrial and freshwater systems (Elser *et al.* 2000) may face not only energetic constraints on growth and reproduction, but also limitation of essential elements (e.g. nitrogen and phosphorus). Recent work on the common zooplankton *Daphnia* in freshwater systems has shown that food quality, which is measured as the relative phosphorus and carbon content, has a significant effect on life-history features and demographic rates (e.g. Urabe & Watanabe 1992; Sterner *et al.* 1993; Sundbom 1997). However, many unanswered questions remain concerning how food quantity and food quality interact to modify the dynamics of plant–herbivore systems.

Theory on the interaction between food quantity and food quality has predicted some intriguing possibilities for the dynamics of plant–herbivore systems. Andersen (1997) developed such a predator–prey model for *Daphnia*–algal systems by considering how phosphorus limitation in the prey combined with potential carbon and phosphorus limitation in the predators alters their dynamics. Depending on the assumptions associated with phosphorus regeneration, herbivore stoichiometry and phosphorus inputs (e.g. closed versus open systems), Andersen (1997) demonstrated that these models produce a rich array of dynamics. One set of predicted dynamics is a stable equilibrium governed by carbon-limited growth in the predator, which produces a pattern of high predator abundance and low prey abundance. This

pattern is commonly predicted by *Daphnia*–algal models that consider only food quantity (e.g. Rosenzweig 1971; Nisbet *et al.* 1989; Kretzschmar *et al.* 1993; McCauley *et al.* 1996). A second set of population dynamics predicted by the model results from phosphorus-limited growth in the predator and produces exactly the opposite population pattern: very high prey abundance and low predator abundance. In Andersen's (1997) model, these phosphorus-limited dynamics were predicted in two cases, one from an unstable equilibrium that ultimately leads to herbivore extinction and, in the second case, via long-phased transition dynamics with herbivore persistence. This particular pattern of high prey abundance and low predator abundance arises in models that consider the effects of both food quantity and food quality (Andersen 1997; Kooijman 1998; Muller *et al.* 2001) from phosphorus limitation of herbivore growth.

Despite the fact that these plant–herbivore models predict multiple dynamics for a single predator–prey system, there is very little experimental evidence for the existence of such patterns. In fact, the only evidence comes from Sommer's (1992) pioneering study where food quality effects were induced by feeding severely phosphorus-limited algae to *Daphnia* populations. By changing the food quality, Sommer (1992) demonstrated that *Daphnia*–algal populations could display the two extreme dynamic patterns predicted by food quantity–quality models. However, these experiments were carried out with a non-dynamic system (i.e. 'static' press experiments with no feedback between predator and prey) and with unrealistically severe phosphorus limitation, thereby potentially invoking energy limitation as well as mineral limitation (Van Donk *et al.* 1997). Such severe phosphorus limitation does not occur in natural systems. Hecky *et al.* (1993) surveyed 51 lakes worldwide and found that, while most of the lakes surveyed would be phosphorus limited, very few would be severely phosphorus limited. Non-severe

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(mild) phosphorus limitation has a much different effect on *Daphnia* demographic rates from severe phosphorus limitation and will probably change how phosphorus limitation affects population dynamics (Sterner *et al.* 1993).

We designed our experiments in order to test for the existence of these alternative dynamics in fully interactive predator–prey systems and under nutrient levels that would induce mild phosphorus limitation. We set up *Daphnia* and algal communities in mesocosms and allowed them to grow and interact without any further addition of nutrients or organisms. Thus, the predators could set their own prey level dynamically, and vice versa. We first inoculated the algal populations into herbivore-free environments and allowed them to establish. We then inoculated the mesocosms with a small number of *Daphnia* in order to test for invasibility and examined the propensity of the populations for displaying the two patterns. In one treatment we inoculated replicate mesocosms using one of three different *Daphnia* clones, each of which was known to have different population growth rates. We hypothesized that the clone with the smallest population growth rate would allow the algal population to grow to higher levels and have a greater tendency to show food quality effects. In order to mimic the initial conditions found in natural communities, we also established mesocosms with multiclonal *Daphnia* populations. We hypothesized that the dynamics of the multiple-clone populations should be within the range of dynamics observed for the three single-clone populations from which they were composed.

2. METHODS

(a) *Experimental methods*

We carried out the experiments in 80-l mesocosms with edible ($< 30\ \mu\text{m}$) green algae and three distinct clones of *Daphnia pulex*. The temperature was maintained at $15\ ^\circ\text{C}$ by heat exchangers beneath the mesocosms. A 12 L:12 D cycle provided $75\ \mu\text{E s}^{-1}\text{m}^{-2}$ of photosynthetically available radiation. Water was collected from the South Saskatchewan River, filtered through a $1\ \mu\text{m}$ filter and enriched with $10\ \mu\text{g l}^{-1}$ phosphorus (as KH_2PO_4) and $400\ \mu\text{g l}^{-1}$ nitrogen (as $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ and NaNO_3). The algal inoculum was a mix of *Scenedesmus obliquus*, *Selenastrum capricornatum*, *Chlamydomonas* spp. and *Chlorella vulgaris* at a final concentration of $79\ \text{cells ml}^{-1}$ in the mesocosms. All *D. pulex* clones were isolated from shallow ponds in Alberta, Canada (2H and 11H were from ponds in a warm region and 8M from a cooler region). Three replicate tanks were inoculated with single-clone populations for each of clones 2H, 11H and 8M. Another three replicate tanks were inoculated with equal proportions of all clones in order to produce the multiple-clone populations. All tanks were inoculated with 290 adult *Daphnia* staggered over two weeks, beginning five days after algal inoculation. There was no subsequent addition of nutrients, algae or *Daphnia*.

The sides and bottoms of all tanks were scraped daily in order to prevent the build up of bacteria. In order to retain nutrients in the water column, we used the regeneration procedure of McCauley *et al.* (1999). This was done once a week. All enumerations were performed twice a week. Chlorophyll *a* was measured as an estimate of algal abundance. Samples were taken by siphoning a 200-ml volume from the tank and passing

it through a $35\ \mu\text{m}$ mesh in order to remove *Daphnia*. Chlorophyll *a* was then measured using the methods of Watson *et al.* (1992). Weekly algal samples were also preserved in Lugol's solution and species composition was determined by subsample counts on an inverted microscope. In order to enumerate *Daphnia*, two 1-l samples were taken from each tank after mixing and passed through a $35\ \mu\text{m}$ mesh. *Daphnia* were then counted under a dissecting microscope, placed into size classes and returned to the tank. *Daphnia* were enumerated into the following size classes: less than 1.0, 1.0–1.4, 1.4–2.0, 2.0–2.5 and more than 2.5 mm. Juvenile *Daphnia* are shorter than 1.4 mm whereas adults exceed 1.4 mm in length. *Daphnia* biomass was calculated using the same relationship as McCauley *et al.* (1999). All statistical analyses were done in SAS v. 8.0 (Cary, NC, USA). Unless otherwise specified, the critical *p*-value was adjusted for multiple contrasts using the Dunn–Sidak method (Sokal & Rohlf 1995).

(b) *Interval choice*

We analysed periods of population growth and periods of constant population density separately. The end of the growth phase was considered the first highest *Daphnia* peak (more than $0.8\ \text{mg carbon l}^{-1}$) and the beginning of the growth period was considered as the point at which the algae began to decline sharply. These criteria were chosen phenomenologically, but prior to any analysis on the resulting intervals.

(c) *Growth rate estimates*

We estimated the instantaneous *Daphnia* population growth rates by assuming exponential growth between successive sampling periods (Taylor & Slatkin 1981). The instantaneous growth rate *r* was calculated for the interval between sampling periods (usually three to four days) as

$$r = \frac{(\ln(N_{t+1}) - \ln(N_t))}{(\text{day}_{t+1} - \text{day}_t)}, \quad (1)$$

where N_t is the total number of *Daphnia* at sampling interval *t*.

(d) *Mortality rate estimates: the egg ratio method*

The egg ratio method can be used for estimating mortality rates as long as a number of assumptions are met (Taylor & Slatkin 1981). These assumptions require that the population has a stable age structure, all stages (including eggs) have the same mortality rates and that their birth and death rates are constant over time. We used the egg ratio formula from Paloheimo (1974) because of its robustness against violations of the assumptions (Taylor & Slatkin 1981). The birth rate *b* is given by

$$b = \frac{\ln\left(\left(\frac{E_t}{N_t}\right) + 1\right)}{D}, \quad (2)$$

where E_t is the number of eggs at time *t* and *D* is the egg development time. We used $D = 2.5$ days, which is the average duration of an adult instar (McCauley *et al.* 1996). The mortality rate *d* was calculated by averaging the birth rate over the sampling interval (in order to match the growth rate) and subtracting the growth rate from it. In order to ensure the validity of our results, we also used a population surface method for calculating mortality rates.

(e) *Mortality rate estimates: population surface method*

This method is detailed in Wood (1994 and references therein) and fits a stage–time surface to the population data, from which

Figure 1. Temporal trends in *Daphnia* biomass, chlorophyll *a* and eggs per female for 8 out of the 12 tanks. The grey area denotes the transition period. The dynamics after the transition period are considered the high HBD and the dynamics before considered the low HBD. (a) Tanks that were dominated by the high HBD and (b) tanks with evidence of the low HBD.

the mortality rates are calculated. Some advantages of this procedure are that all of the data are used simultaneously (thereby reducing the effects of noisy data), mortality is estimated for each stage and the mortality rates are constrained to be positive and, thus, biologically reasonable (Wood 1994). We used a program supplied by S. N. Wood (available at <http://www.ruwpa.st-and.ac.uk/simon/mort.html>) and fit the surface using ordinary cross-validation. Since most of the adults were in the first adult stage class we lumped all of the adults into a single stage in order to prevent numerical instabilities in the fitting procedure. This left us with four stages: egg, juvenile 1, juvenile 2 and adult. The development time through the egg, juvenile 1 and juvenile 2 stages must be provided for this method. We estimated the development times independently from the chlorophyll *a* abundance in each tank. In order to do this, we first estimated algal carbon using the formula $\text{carbon (mg l}^{-1}\text{)} = 0.032 \times \text{chlorophyll } a \text{ (}\mu\text{g l}^{-1}\text{)}$ (Reynolds 1984). We then calculated the stage duration using the relationship between the algal carbon and development

time from McCauley *et al.* (1990). This was smoothed (exponential smoothing) and bracketed between eight days and 45 days in order to ensure that individuals could not age faster than one day per day (Wood 1994). We made the assumption that the three stages (egg, juvenile 1 and juvenile 2) have the same duration and calculated the stage duration as one-third of the development time. Food quality may be expected to modify the development time relationship from McCauley *et al.* (1990). However, studies have shown that this effect is small compared with food quantity (e.g. Kilham *et al.* 1997; Lurling & Van Donk 1997). We tested the sensitivity of our results for populations experiencing low food quality by recalculating mortality rates with double the estimated development time.

3. RESULTS

We observed two distinct and contrasting patterns in *Daphnia*–algal population dynamics at 15 °C. The first of

these patterns was characterized by a high predator biomass and low prey biomass and can be seen in the four populations shown in figure 1*a*. We refer to this as the high herbivore biomass dynamics (high HBD). The remaining four replicate tanks displaying the high HBD were not included for clarity, but have the same patterns as those shown in figure 1*a*. All populations that initially started at the high HBD were composed of a single clone (either clones 2H, 8M or 11H) and, thus, had no genetic diversity. In stark contrast to the first pattern, the second pattern was characterized by a low predator abundance and high prey abundance, which we refer to as the low herbivore biomass dynamics (low HBD). Four of the experimental tanks displayed the low HBD for all or part of their time-series, as seen in figure 1*b*. With the exception of one tank that became extinct after 120 days (top panel in figure 1*b*), all of the populations at the low HBD eventually shifted to the high HBD. Three out of the four low HBD populations began with genetically diverse populations (i.e. composed of equal proportions of all three clones). The fourth tank, which exhibited the low HBD for the shortest period of time, was a single-clone population. Between the low and high HBD, the populations underwent a period of strong growth. Another growth period occurred between inoculation and the high HBD. Since we were primarily interested in understanding the patterns of HBDs, we analysed these growth periods separately. These are highlighted by a grey background in figure 1 and are hereafter referred to as ‘transition periods’.

The rules used to identify the transition periods were phenomenological, but their appropriateness is confirmed in figure 2*a*. Here the growth rates for both patterns of HBDs are not significantly different from zero (ANOVA with three contrasts, adjusted $p \gg 0.017$), whereas the growth rate for the transition period was significantly higher than either pattern (ANOVA with three contrasts, adjusted $p < 0.017$). Figure 2*a* also shows the average growth rate for each clone (2H, 8M or 11H) separately. Interestingly, while each clone had similar growth rates at the high HBD, they differed substantially during the transition phase. Clone 2H had the highest growth rates at a low chlorophyll *a* level. Clone 8M had lower growth rates than clone 2H but at the same low chlorophyll *a* level. Clone 11H had the lowest growth rate of all and at consistently higher chlorophyll *a* values. In fact, the combination of the growth rate and chlorophyll *a* level for the 11H clones shared a similar region as the tanks with the low HBD. Figure 2*b* clearly shows the different patterns of average *Daphnia* and algal abundance for the three regions. The two patterns of HBD are separated by both predator and prey abundance (ANOVA and Tukey’s HSD test, $p < 0.05$). The low HBD occupy the low predator and high prey region and the high HBD occupy the high predator and low prey region. The growth period is significantly different from both patterns of HBDs by predator abundance and from the low HBD by prey abundance (ANOVA and Tukey’s HSD test, $p < 0.05$). The transition from the low HBD through the growth phase to the high HBD can be seen in figure 2*b* by following the multiple-clone symbols. The high HBD are quantitatively similar for all tanks, regardless of whether the population was growing from the low HBD or had

Figure 2. (*a*) The average *Daphnia* growth rates for multiple-clone populations (squares) and the single-clone populations 2H, 8M and 11H (triangles, circles and hexagons, respectively). The shading indicates the low HBD, the transition period or the high HBD (black, grey and white, respectively). The arrow indicates the single 11H tank that began at the low HBD. (*b*) The open grey-outlined circles connected by grey arrows indicate the average *Daphnia* biomass and chlorophyll *a* for each period. The range of duration for each period is indicated. Black-outlined symbols indicate the genetic diversity of the *Daphnia* populations (circles for single clones and squares for multiple clones). The shading of the symbols is the same as in (*a*).

reached the high HBD directly after inoculation. The duration of each period for the populations is also shown in figure 2*b*. The transition period was always very short, ranging from 14 to 17 days, whereas the high HBD persisted to the end of the experiment, which was on average longer than 80 days. In contrast, the low HBD had a highly variable persistence time, ranging from 17 to 120 days. Furthermore, there was a strong linear correlation between the persistence time of the low HBDs and the initial chlorophyll *a* abundance, where higher initial chlorophyll *a* abundance correlated with a longer persistence time ($p < 0.0001$) (Pearson correlation coefficient, > 0.98).

Figure 3 shows the average number of eggs per female and the average mortality rates for the two patterns of HBD and the transition period. The high and low HBD can be distinguished by fecundity, as seen in figure 3*a* where the high HBD is characterized by a very low number of eggs per female and the low HBD by high egg production. In fact, the low HBD had the same number of eggs per female as the growth period (ANOVA

Figure 3. (a) The average number of eggs per female and (b) the average per capita *Daphnia* mortality rate by chlorophyll *a* for each period. The symbols and shading are as in figure 2b. The average per capita *Daphnia* mortality rate was calculated using the egg ratio method.

$p \gg 0.05$) but without the corresponding growth. This suggests that the populations at the low HBD suffered a high degree of mortality. The mortality rates calculated using the egg ratio method of Paloheimo (1974) are shown in figure 3b. The low HBD did indeed have a significantly higher mortality rate at the higher algal abundance than the high HBD (ANOVA and Tukey's HSD test, $p < 0.05$). The transition periods are not shown because the mortality rates were either negative or very high, which suggests a violation of assumptions.

In order to validate these results, we also estimated mortality rates using the population surface methods of Wood (1994) (figure 4a). The average mortality rates of the low and high HBD (figure 4a) agreed very well with those estimated using the egg ratio method (figure 3b), giving us confidence in the results. The other advantage to using this method is that the mortality rates were calculated for each stage in the population (figure 4b). They revealed that the mortality rates for all of the population stages at the low HBD were significantly higher than the high HBD (ANOVA with five contrasts, adjusted $p < 0.01$). In contrast, the mortality rates of the egg and juvenile stages at the high HBD were almost zero (ANOVA with five contrasts, adjusted $p \gg 0.01$) and only the adults suffered any significant mortality (ANOVA with five contrasts, adjusted $p < 0.01$). The growth period had the same adult mortality rate as the high HBD (ANOVA with five contrasts, adjusted $p \gg 0.01$), but

Figure 4. (a) The average per capita *Daphnia* mortality rate for each period calculated using the surface methodology. The symbols are as in figure 2b. (b) The average per capita *Daphnia* mortality rate broken up by stage class. The symbols represent the averages of all tanks in that period. The symbol shading is as in figure 2a. The error bars are 95% confidence intervals. The grey circle below the black hexagon represents the mortality rate when the development time is doubled.

suffered more mortality in both juvenile stages (ANOVA with five contrasts, adjusted $p < 0.01$).

The estimated development times for the low and high HBD were eight days and 33 days, respectively. As discussed in §2, we tested the sensitivity of our mortality estimates of the low HBD to the estimated development time by recalculating mortality rates with twice the development time. These are shown as grey circles in figure 4b. Doubling the development time of the low HBD to 16 days caused the mortality rates to drop in all stages, but still remain much higher than the high HBD. This means that the low HBD had a consistently higher mortality rate than the high HBD, a result that was not sensitive to the development time.

We estimated cell abundance and species composition over time from preserved algal samples in the three tanks that showed the most dramatic chlorophyll *a* shifts. The enumeration revealed that the algal population was dominated (greater than 95% cell abundance) by a single species (*Selenastrum capricornatum*) for the entire experiment. The algal abundances, as estimated from counts of preserved samples and from chlorophyll *a* measured during the experiment, were significantly correlated over

time ($p < 0.0001$) (Pearson correlation coefficient, > 0.97), demonstrating that the observed shift in algal abundance was a result of the predator–prey interaction and not due to shifts in algal species composition or cellular chlorophyll *a*. Most of the initial phosphorus added to the mesocosms ($10 \mu\text{g l}^{-1}$) remained at the end of the experiments, with very little variability between mesocosms. The average total phosphorus in the mesocosms at the end on the experiment was measured as 8.3 mg l^{-1} .

4. DISCUSSION

Our results clearly show the existence of two distinct dynamic patterns from a single, predator–prey system. The first, the high HBD, had a high predator biomass and low prey biomass. The second pattern, the low HBD, had a low predator biomass and very high prey biomass. The demographic difference between the two patterns can be visualized by following the patterns of cohort succession in each. At the high HBD, the cohort began with a small number of eggs produced by the population (figure 3*a*). There was almost no mortality of eggs or juveniles (figure 4*b*) and slow development into adults. As adults they reproduced infrequently and eventually died at an older age. A different pattern emerged for populations in the low HBD. Here, a large number of eggs were produced (figure 3*a*). The high egg and juvenile mortality allowed very few of these eggs to make it to the adult stage (figure 4*b*). Those that did grew very rapidly. Once adults, they had a very short time for reproducing before succumbing to the high adult mortality. These patterns of cohort succession and of predator and prey abundance demonstrated that the two patterns of HBDs have very different predator–prey dynamics. In order to interpret the dynamics of these two patterns further, we took a comparative look at published experimental results and predator–prey models.

The characteristics of the high HBD pattern are commonly seen in *Daphnia*–algal predator–prey dynamics under a variety of experimental and natural conditions (McCauley & Murdoch 1987, 1990). The low egg production and algal abundance per *Daphnia* suggests that the predator demographic rates in our populations were strongly influenced by carbon limitation. Many predator–prey models (e.g. McCauley *et al.* 1996; Andersen 1997) have predicted population dynamics with the same characteristics as the high HBD pattern. When these models predict the qualitative pattern of the high HBD, it results from a stable equilibrium dominated by carbon limitation in the predator. Our results were consistent with a stable equilibrium because all persistent populations ended up at the high HBD and none showed any tendency towards a different pattern once there. These comparisons demonstrate that the high HBD pattern of high predator biomass, low prey biomass and low egg production is consistent with the carbon-limited predator dynamics commonly seen in *Daphnia*–algal predator–prey systems and with the stable carbon-limited equilibrium commonly predicted by predator–prey models.

In contrast, the low HBD pattern of high prey biomass, low predator biomass and high concurrent egg production by predators has never, to our knowledge, been observed before in predator–prey systems. Interest-

ingly, predator–prey models that consider the effects of food quantity as well as food quality do predict a pattern of high prey biomass and low predator biomass (Andersen 1997; Muller *et al.* 2001). Fortunately, there is extensive literature on food quality effects for *Daphnia* that we can use for determining whether the low HBD is consistent with predator–prey dynamics influenced by food quality (Sterner & Hessen 1994). Of the possible food quality effects, phosphorus limitation is believed to be the most important to *Daphnia* (Sundbom 1997) and is typically expressed as the phosphorus to carbon (P:C) ratio in algal prey. We measured the total phosphorus at the end of the experiments and calculated the maximum ratio during the low HBD as $\text{P:C} = 0.007$. This ratio is sufficiently low to have a significant impact on the demographic rates of *Daphnia* (Urabe & Watanabe 1992; Van Donk & Hessen 1993). Support for the hypothesis that phosphorus limitation was an important mechanism in maintaining our low HBD comes from a chemostat experiment by Sommer (1992), who found the same low predator and high prey dynamics that we did by manipulating the algal P:C ratio. The population dynamics were identical to the pattern of our low HBD with the exception of egg production, which was very low in Sommer's (1992) populations, probably due to the severity of phosphorus limitation imposed. Sommer's (1992) populations were at a P:C ratio of 0.001. Such severe phosphorus limitation causes the cell morphology of many green algae to change, rendering them to indigestible to *Daphnia* (e.g. Van Donk *et al.* 1997). Therefore, Sommer's (1992) populations were probably carbon limited as a result of significantly reduced digestibility, as well as being phosphorus limited because of the low algal P:C ratio. On the other hand, mild phosphorus limitation has a large effect on *Daphnia* demography (Sterner *et al.* 1993) but, because it does not affect algal digestibility, *Daphnia* populations will not be carbon limited with abundant algae. The P:C ratios calculated in our tanks put our populations specifically within the range of mild phosphorus limitation as opposed to severe phosphorus limitation (Urabe & Watanabe 1992; Sterner *et al.* 1993; Van Donk & Hessen 1993; Lurling & Van Donk 1997). This is further supported by the high egg production, which could not occur under carbon-limited conditions. The P:C ratio calculated in our tanks and the similarity of our results with Sommer's (1992) results, support the idea that the low HBD pattern is a result of dynamics governed by phosphorus limitation in the predator. Predator–prey models such as Andersen's (1997), which consider both food quantity and quality, predict population dynamics with the same pattern as the low HBD. Andersen's (1997) model predicted phosphorus limitation dynamics under two circumstances: (i) an unstable equilibrium that leads to herbivore extinction and (ii) long-term transition dynamics between small inoculations and the common high HBD pattern that can last for periods longer than the growing season in temperate zone lakes. The population dynamics predicted have very high prey abundance, low predator abundance and are produced solely as a result of phosphorus limitation. Therefore, the low HBD pattern, which we have argued is primarily a result of phosphorus limitation, is qualitatively consistent with the

population dynamics predicted by food quantity–quality models in parameter regions where herbivores and their prey persist in the system.

We have demonstrated a strong consistency between the patterns of our populations, the likely underlying dynamic mechanisms (i.e. carbon versus phosphorus limitation) and those predicted by food quantity–quality models. However, our present study cannot distinguish between dynamics that result from a stable equilibrium or long-duration transition dynamics. Further experiments involving perturbations are needed in order to identify the validity of predictions from particular food quality models.

An intriguing result from our experiments was the nature of the populations that tended to exhibit the low HBD versus the high HBD. Only one out of the nine single-clone populations showed any evidence of the low HBD, and only did so for a short time. We hypothesized that the clone with the slowest population growth rate would allow the prey to reach the highest levels and, therefore, have a greater chance of experiencing negative food quality effects. The initial growth phase from inoculation to the high HBD (figure 2a) can be used to compare each clones' population growth rate. Clone 2H had a much higher growth rate than either of the other two clones. Clone 8M had a lower growth rate than 2H, but at the same chlorophyll *a* level. This suggests that clone 8M may have been as successful as clone 2H at grazing the algal population but did not convert it to population growth. As circumstantial evidence, clone 8M had almost double the ephippial egg production of the other two clones, which may account for some of the lost energy (Lynch 1983). Clone 11H had the same low growth rate as 8M, but at a higher chlorophyll *a* value. Consistent with our hypothesis, this is the only single clone that showed evidence of the low HBD. Interestingly, the multiple-clone populations were all initially dominated by the low HBD. We originally hypothesized that multiple-clone populations should exhibit dynamics that were within the range found for the component single-clone populations, but this was certainly not the case. We cannot attribute these results to an experimental artefact because the inoculations for all tanks were performed at the same time with the same protocol and from the same single-clone stock tanks. One speculative explanation is that the initial population growth rates of the multiple-clone populations were lower than the single-clone populations, thereby allowing the algae to grow with less grazing pressure. This could have occurred if there was interference competition between the clones. Interference competition mediated by chemical signals has been observed between copepod species (Folt & Goldman 1981). However, interference competition has not been observed between *Daphnia* species (Burns 1995), nor has it been observed between clones of *Daphnia magna* (Mitchell 1997). Regardless of what caused the multiple-clone populations to display the low HBD, a small effect may be sufficient for a population to fall into the low HBD rather than the high HBD (Sommer 1992; Andersen 1997).

In conclusion, we found two fundamentally different dynamics from a single predator–prey system under conditions similar to natural communities. We found strong evidence that one set of dynamics was a result of

food quantity effects and the second a result of food quality effects, which were maintained by mild phosphorus limitation in the predator. These results provide an important step towards linking the effects of nutrient limitation on herbivores, as determined from static laboratory experiments and the importance of food quality for zooplankton dynamics and community structure in natural lakes and ponds.

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