

Overcrowding, food and phosphorus limitation effects on ephippia production and population dynamics in the invasive species *Daphnia lumholtzi*

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Abstract *Daphnia lumholtzi* has been very successful in colonizing North America since its appearance in Texas in 1990. Although previous studies have sought to link its success as an invasive species with various aspects of its population biology, there is little experimental data linking the invasion success of *D. lumholtzi* with its autecology, specifically its reproduction strategy. In this study we sought to link food quality and quantity to diapause in *D. lumholtzi* through a variation in phosphorus (P) content of algae, food quantity, and light level. We also assessed the effect of *Daphnia* peak population densities on reproductive rates and production of resting eggs. We found that when food is abundant, per capita ephippia production may be limited by P, but under food limitation conditions, there is no significant effect of food quality on ephippia production. Our results suggest that a combination of food quality/quantity and population density may work

together to induce the production of resting eggs in this invasive species.

Keywords Resting eggs · Diapause · Invasibility · Food quality · Food quantity · Cladocera

Introduction

For many organisms, dormancy provides an effective method for avoiding adverse conditions while ensuring genetic variability. Plants and insects both utilize varying forms of dormancy to persist through conditions that would be fatal to active individuals. Similarly, many species of freshwater and near shore marine zooplankton produce long-lived dormant eggs that accumulate in sediment banks (analogous to seed banks; Hairston et al., 1995; Cáceres, 1998; Cáceres & Tessier, 2004) and enhance the persistence ability of many zooplankton species (el Moghraby, 1977; Hairston et al., 1995; Brendonck & De Meester, 2003; Mergeay et al., 2004).

Many zooplankton species, such as monogonont rotifers and in particular most cladocerans, can shift from asexual, clonal reproduction to resting eggs produced via sexual reproduction (Innes & Singleton, 2000) in response to environmental cues such as overcrowding (Gilbert, 2003, Schroder & Gilbert, 2004), photoperiod and food effects (Gilbert & Schreiber, 1995; Deng, 1996), maternal control (Alekseev &

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Lampert, 2001), predator kairomones or feces (Slusarczyk, 2004; Slusarczyk & Rygielska, 2004; Slusarczyk et al., 2005), and the presence of competitors (Johnson & Havel, 2001). This shift to sexual reproduction often represents a bet-hedging strategy (Ellner et al., 1998; Chesson, 2000; Cáceres & Tessier, 2003), allowing individuals to produce dormant offspring that will hatch under favorable conditions. While there is an immediate cost to putting resources into dormant stages that will not immediately join the population, this is outweighed by the benefits of a higher proportion of offspring surviving the current adverse conditions.

Since zooplankton are often the crucial link between producers and higher trophic levels in aquatic food webs (e.g., Brooks & Dodson, 1965; Carpenter & Kitchell, 1984; Williamson & Stoeckel, 1989), factors which influence the induction of diapause may have strong effects on the biotic interactions in these systems, particularly in cases where exotic zooplankton are invading new habitats. *Daphnia lumholtzi* Sars, a recent invader in the zooplankton communities of North America, is one of the many cladoceran species to employ diapause as a reproductive strategy. First detected in North America in 1990 in a reservoir in Texas (Sorensen & Sterner, 1992), *D. lumholtzi* has since spread from Texas to the Great Lakes (Havel et al., 1995; Muzinic, 2000).

Growth and population density of *Daphnia* are generally determined by the availability and quality of food, although abiotic factors can also be important (e.g., Acharya et al., 2004). Phosphorus (P) and nitrogen (N) levels have been shown to have a strong influence on food quality for freshwater zooplankton. For example, *Daphnia* growth has been shown to correlate with algal P content when food P is low (Gulati & Demott, 1997; Acharya et al., 2004), and P supplementation experiments have shown that at least some of the reduction in growth is a direct result of P deficiency (DeMott et al., 1998; Elser et al., 2001; Boersma & Kreutzer, 2002). Since growth rate can also affect age at first reproduction, food quality has short- and long-term consequences for reproductive output, adult body size, and other key aspects of species' life history (Arendt, 1997). Although many studies have been devoted to understanding the growth rate and resource allocation in *Daphnia*, little is known about the role nutrients such as P and N content in food play in ephippia production.

Ephippia production in *Daphnia* is initiated when the cues for diapause are detected. Like most other species of *Daphnia*, *D. lumholtzi* produces two resting eggs per fertilized female, which are enclosed in a hard ephippium case. Sexual females produce ephippium, while other females produce broods containing the males necessary for fertilization. The fertilized ephippium is then released into the water column to await hatching cues. A recent study by Acharya et al. (2006) showed that *D. lumholtzi* produced ten times more ephippia than *D. pulicaria* and *D. magna* under similar food conditions. Also, *D. lumholtzi* had relatively higher body %RNA than the other two species. The Growth Rate Hypothesis (GRH; Elser et al., 2003) predicts that %RNA, %P, and growth rates are correlated under P-limited conditions. Therefore, it is possible that P content and food availability in the environment may be related to resting egg production and invasion success.

The effect of light level could potentially impact the production of resting eggs. Photoperiod change is known to induce diapause in *Daphnia* (Deng, 1996) and alter diel vertical migration in association with predator presence. Light level could potentially intensify the effects of predation by visual predators for females carrying the dark ephippium. However, Slusarczyk et al. (2005) and Alekseev (2004) found that high-light level increased resting egg production when fish kairomones were present while no resting eggs were produced in complete darkness (Alekseev, 2004).

In this study we sought to link food quality and quantity to ephippia production in *D. lumholtzi* through a variation in phosphorus (P) content of algae, food quantity, and light levels. We also assessed the effect of *Daphnia* densities on reproductive rates and production of ephippia. We hypothesized that diapause in *D. lumholtzi* would be linked with food quality and quantity as well as population density via the production of ephippium. In order to eliminate any confounding effects of light level, we also ran a separate experiment to look at the effect or lack thereof of light levels in ephippium production.

Methods

Cultures and chemostat

The experiments were conducted with *D. lumholtzi* collected from the Ohio River at Ohio River

Kilometer 933 and established in stock cultures at the University of Louisville (Louisville, KY, USA). Laboratory experiments were conducted on a large number of neonates of approximately the same age, size, and condition born from a single mother (one clonal line) to avoid possible confounding effects of genetic differences between clones. To produce our study cohorts, offspring born from a single mother from a stock culture was isolated and grown individually on high concentration (1.5 mg C l^{-1}) of the algae *Scenedesmus* until reproduction began. About 60–80 third clutch neonates were then separated and grown individually in 250-ml jars with sufficient, high-quality food. These animals were then transferred to clean jars at regular intervals, and neonates (within 24 h of birth) from the third and subsequent clutches of these animals were used for the experiments.

The green alga *Scenedesmus acutus* was grown in a chemostat under two conditions of P and N supply. P-rich *Scenedesmus* was grown on filtered ($0.45 \text{ }\mu\text{m GF/F}$) and autoclaved Ohio River water modified to contain at least $1,000 \text{ }\mu\text{M N}$ and $50 \text{ }\mu\text{M P}$ (molar N:P ratio 20) in batch cultures. P-poor *Scenedesmus* was grown on filtered ($0.45 \text{ }\mu\text{m GF/F}$) and autoclaved Paramount Lake (an oligotrophic lake in Oldham County, Kentucky, with typical dissolved N and P values of less than 100 and $5 \text{ }\mu\text{M}$) water modified to contain $5 \text{ }\mu\text{M P}$ and $500 \text{ }\mu\text{M N}$ (N:P 100) and grown under increased light intensity (Acharya et al., 2006). The concentrations and C:N:P ratio of algae from the chemostats were monitored throughout the experiment. Algal samples on filters were dried in an oven at 60°C and held in a desiccator until analysis for C and N content (using Perkin–Elmer model 2400 elemental analyzer) and P content (using persulfate oxidation followed by the acid molybdate technique; APHA, 1998). High P *Scenedesmus* had biomass C:P ratio (molar) of approximately $135.6 (\pm 5.8)$, while low P *Scenedesmus* had a C:P ratio of $695.8 (\pm 25.8)$.

P-limited experiment

P-limited experiments examined the effects of two diets (high P and low P) at two food levels on the population and ephippia production of *D. lumholtzi*. A large cohort of neonates of *D. lumholtzi* was collected as described above. *Daphnia* were grown in 250-ml flasks with 225 ml of filtered ($0.45 \text{ }\mu\text{m}$) Paramount Lake water. There were a total of 12

treatment combinations ($2 \times 2 \times 3$): two diet treatments at two food levels (hereafter “high P & Q,” “high P low Q,” “low P high Q” and “low P & Q,” where P = phosphorus and Q = food quantity) at three initial *Daphnia* densities of 10, 5, and 1 individuals per flask. Each treatment had four replicates. High and low food levels were 1.5 and 0.2 mg C/l, respectively. All *Daphnia* from each treatment was counted twice weekly by pipetting the animals and transferring them to new flasks. After counting, half of the media was replenished by filtering the animals through $20 \text{ }\mu\text{m}$ Nitex mesh filters. Spent media at the peak culture density was tested for NH_4 levels to ensure levels were below toxicity thresholds. Typical toxicity level for *Daphnia magna* has been reported as 2.94 mg/l for 96 h-acute, and 0.6 mg/l for 21 d-chronic (Gersich & Hopkins, 1986). During each population count any ephippium found was counted and removed. Random ephippia were broken and examined under the microscope to confirm that resting eggs were present. Experimental jars were maintained under 14:10 h light:dark cycle and a temperature of 25°C for 44 days.

Light level experiment

We also conducted an experiment using a similar design to ensure that our results were not an artifact of the light levels under which the experiment was conducted. There were three treatments (dark, medium, and high light), each with three replicates and a starting density of five individuals in the light level experiment. All treatments were fed high P food only at high concentrations (1.5 mg C/l ; high P high Q). Animals at high-light treatments were kept in a growth chamber under fluorescent tubes with high-light level ($16,515 \text{ lumens/s}$) at 14:10 h light:dark cycle, medium-light treatments were kept at ambient fluorescent room light (954 lumens/s) at 14:10 h light:dark cycle, and low-light treatments were kept in a 24 h-dark cabinet. The rest of the experimental procedures and data collection followed the same pattern as the P limitation experiment described above except that the light level treatments were discontinued after 25 days.

Statistical analysis

We used analysis of covariance (ANCOVA) with days (on which the population was counted, e.g., 1, 4,

7 up to 44) as covariant to assess the effects of food quality and quantity on population numbers and per capita ephippia production. We also ran Tukey honest significant difference (HSD) multiple-comparison tests to identify the treatments where significant differences in population and per capita ephippia production occurred. Three initial starting densities were pooled for statistical analysis which raised the number of replicates to 12 (3 starting densities \times 4 replicates) for each treatment. This was done because there were no significant differences in the size of peak populations for any 1, 5, or 10 initial density. The same statistical procedure was repeated for light level treatments, with one starting density (5 ind.) and three replicates for each treatment.

Results

Populations of animals fed varying quantities of P-limited and P-rich food (P-limited experiments) grew best when the food was P-rich and in abundant quantity (high P & Q) followed by low P & high Q and low Q treatments (Fig. 1). A combined (grouped by the four treatments, with all starting densities

averaged for each treatment) analysis of covariance with time (population count days) as a covariate indicated that population densities and the subsequent ephippia production differed for different food concentrations (high versus low) and types (high P versus low P) in P-limited experiments ($P < 0.001$). In general, peak population density was highest at high P high food concentrations (high P & Q) followed by low P high Q food (Fig. 1). Population densities remained low at the two low food quantity treatments (high P & low Q and low P & Q) and were not statistically different (40–60 ind/l, Tukey LSD pairwise comparison) but were different from both high food treatments (high P & Q, low P & high Q) which in turn were also significantly different from each other (high P & Q: 300–350 versus low P & high Q: 150–200 ind/l, Table 1).

Ephippia production followed a similar pattern with the maximum number of ephippia produced at high P & Q treatment (Fig. 2). Ephippia production declined significantly at low P high Q treatment and there were very few ephippia at both low quantity treatments (high P & low Q, low P & Q). Analysis of covariance showed, as with the population, that the ephippia production followed a consistent pattern:

Fig. 1 Average population density of *D. lumholtzi* at (A) high P & Q, (B) low P high Q, (C) high P low Q, and (D) low P & Q food conditions. All starting densities were averaged for each treatment (Note the scale differences between (A/B) and (C/D))

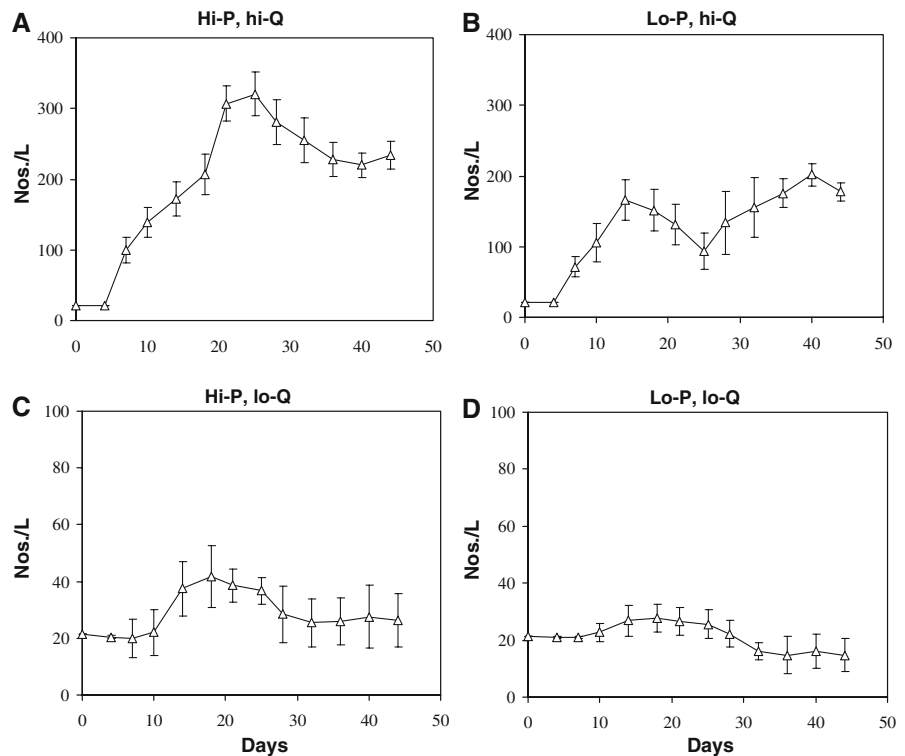
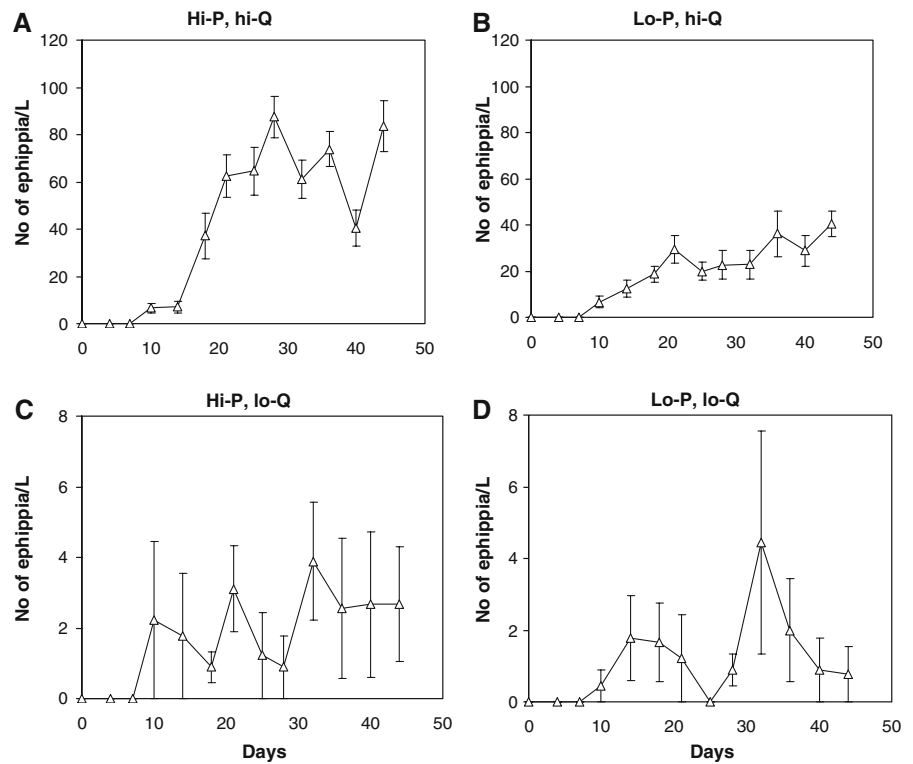


Table 1 Analysis of covariance (ANCOVA) and pair-wise comparison (Tukey LSD) results for treatment effect on population and ephippia production of *D. lumholtzi* for 10, 5, and 1 initial densities

	P values						Pair-wise comparison	
	Population			Ephippia			Population	Ephippia
	10 ind	5 ind	1 ind	10 ind	5 ind	1 ind		
High P & Q	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	A	A
High P Low Q	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	B	B
Low P High Q	<0.001	<0.001	<0.001	0.83	0.19	0.11	C	C
Low P & Q	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	C	C

Age (days) of the experiment was used as covariants for both population and ephippia production

Fig. 2 Average ephippia production of *D. lumholtzi* at (A) high P & Q, (B) low P high Q, (C) high P low Q, and (D) low P & Q food conditions. All starting densities were averaged for each treatment. Please note the difference in scale between the top and bottom panels



both low food quantity treatments were similar but were different from both high P & Q and low P high Q treatments, which were also significantly different from each other (Tukey LSD; Table 1).

Per capita ephippium production was calculated for each treatment for each population using the peak population on each day divided by the number of ephippia present. We found per capita ephippium production was highest at high P high Q (maximum 30–40%) and lowest at low P low Q (10–15%) conditions. On low Q high P food, per capita ephippium production was about 20–25% of the total

population. Analysis of variance showed that per capita ephippium production differed significantly for all four treatments ($P < 0.01$). Furthermore, Tukey LSD pair-wise comparison test indicated that both high quantity treatments were similar but both differed significantly from both low quantity treatments. The high quantity treatments showed a positive correlation between food quality and ephippia production, which was absent under food limitation.

Ammonia levels in all treatments were consistently below known toxicity levels for *Daphnia* species (<0.04 mg/l).

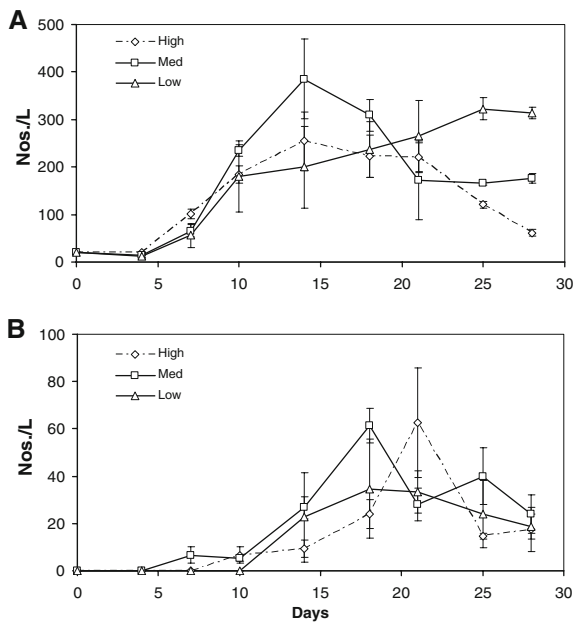


Fig. 3 Average population density (A) and ephippia (released) production (B) of *D. lumholtzi* at high (diamond), medium (square), and low (triangle) light level experiments

The light level experiment showed that animals had a higher population peak in medium (ambient) and dark treatments and a lower population peak in the high-light treatment (Fig. 3). Analysis of covariance showed a significant difference in population patterns (e.g., time taken to peak and crash; $P < 0.01$), with the dark treatment differing from the high-light treatment while the ambient light treatment was similar to both the low- and high-light treatments (Tukey LSD pair-wise comparison). However, there were no significant differences for total ephippia production or per capita ephippium production ($P > 0.1$) between the three treatments.

Discussion

Daphnia lumholtzi population growth followed a typical *Daphnia* population pattern (peaking and crashing; McCauley et al., 1990) and similar data for several other *Daphnia* have been published (George & Edwards, 1974). The responses of *D. lumholtzi* to food quality and quantity were also similar to congeners in previous studies (*D. magna*, DeMott et al., 1998; *D. galeata* and *D. pulicaria*,

Acharya et al., 2004) with both low and high P at limited quantity food resulting in lower population peaks than at abundant food of either P level. There was a significant difference in population growth between P-sufficient and P-deficient food at high quantities suggesting P limitation at abundant food conditions. This is not unexpected as several previous studies have shown that P limitation occurs at high food conditions when the P content is low (Boersma & Kreutzer, 2002). However, contrary to some studies with cladocerans (e.g., Boersma & Kreutzer, 2002; Acharya et al., 2004), *D. lumholtzi* growth rates were not affected by P at limiting food conditions. Sterner & Robinson (1994) observed a similar pattern among *Daphnia obtusa* and our data linking dietary stoichiometry with population growth are consistent with studies done using individual growth rates (Acharya et al., 2004, 2005). This suggests that food quality studies using individual growth rates in *Daphnia* may be as powerful as those done using the more laborious population dynamics approaches.

As with the population growth rates, ephippium production may have been affected by the P content of the food. The number of ephippia produced declined significantly in the low P & high Q treatments (Fig. 2) suggesting that P levels may have played a role in ephippium production. Our experiments suggest that per capita ephippium production (highest number of ephippia over peak population) at high P high Q was nearly double (~25%) that found in the low P high Q (~12%) conditions. This is not surprising as several previous studies have shown that the demand for P and RNA could have implications for the allocation of elements or biochemicals to reproductive or other tissues (Færøvig & Hessen, 2003). For example, RNA level is increased during prenatal embryogenesis (Gorokhova & Kyle, 2002) and the P allocation to eggs depends on food quantity and quality, with consequences on the survival and growth rates of the neonates (e.g., Boersma & Kreutzer, 2002). While the difference for P and RNA demand between parthenogenetic and ephippial offspring has not been experimentally established, our data suggest that the P content in food did not play a role in ephippium production when food was limited, as there were very few ephippia produced under food limitation. Our experiments do not directly distinguish between the effects of food quality versus crowding; it is entirely possible that

the ephippia production was influenced by overcrowding at high food condition. However, our data do show that ephippia production continued even when the culture density was very low and this may suggest that food quality was important in ephippia production.

We observed that the timing of ephippium production in our experiments varied based on starting density but the total number did not change significantly over the length of the experiments. Generally, *D. lumholtzi* in higher quality and quantity food had higher per capita ephippium production in our experiments. High per capita resting egg production has been noted in other invasive zooplankton species. Riccardi et al. (2004) found a high per capita resting egg production (23%) in *D. parvula*, an invasive species from North America first detected in Lake Candia, Italy, in 2002. The ecological explanation of this might be that by producing high numbers of resting eggs, aquatic organisms are able to not only disperse to new environments but also, in effect, disperse through time as conditions in their current environment deteriorate. Thus, cladocerans that produce many resting eggs might have a higher probability of successfully dispersing into new habitats or reappearing later if current conditions become unfavorable.

Our results from the light level experiment suggested that *D. lumholtzi* population growth, but not ephippium production, is affected by light intensity. *Daphnia* grown in the dark and at ambient (natural North American summer) light levels had higher population peaks than the animals at enhanced light level (growth chamber) in our experiment (Fig. 3). There are several possible explanations for these results. This may be the result of *Daphnia*'s predator avoidance response. *Daphnia* were grown in filtered Ohio River water which may still have had residual fish chemical cues (e.g., kairomones) and as a result *Daphnia* did not feed well in the high-light intensity treatment. Similar observations were made by Starkweather (1978). Also, seasonal events and factors correlated to season (e.g., photoperiod) are reliable cues for the induction of ephippium production (Stross and Hill, 1965; Sommer et al., 1986). At the same time, light intensity often causes vertical diel migration in zooplankton as a predator avoidance response (Dodson, 1990) which may deprive *Daphnia* from access to food in the upper water column.

Alekseev (2004) showed that the combination of light and food levels had an impact on *D. pulicaria* diapause induction. Our experiments were not designed to test the effect of food level at different depths; therefore light levels alone or in combination with other cues (e.g., increased C:P ratio) might have caused *D. lumholtzi* to have a reduced population density at high light levels in our data. Urabe et al. (2002) found that, in addition to the effects of UV radiation, increased light level decreases herbivore production due to stoichiometric effects of light/nutrient balance (increased C:P ratio).

In addition to the effects of light, the known cues required to initiate ephippium production include population density, temperature, food quality and quantity, accumulation of metabolic products, chemical cues of predators, etc. (Ferrari & Hebert, 1982; Hebert, 1987; Slusarczyk, 1995; Cáceres, 1998). Incubation conditions (light, photoperiod, temperature, media, and likely presence of fish chemical cues in source water, food quality and quantity) were similar in all our experiments, and we did not detect any elevated levels of metabolic products such as ammonia. Therefore, since food quality and quantity were equivalent between light treatments, crowding (culture density) appears to be the most likely cue in this case.

Our data also suggest that ephippium production for *D. lumholtzi* may also be linked to food quality and quantity. Some species such as *D. parvula* generally produce more resting eggs than some common species in Europe (*D. pulicaria*, *D. magna*; Riccardi et al., 2004), which might be due to their differing genetic or physiological characteristics. However, Riccardi et al. (2004) found that ephippium production in *D. parvula* began when the population density was low and food quantity was high. Our data indicate that the role of diet (food quantity or quality) might have affected the extent of ephippium production in *D. lumholtzi*. It is also possible that once the cue is detected (from somewhere else) the food conditions will then control the amount of ephippia produced due to high requirement for resource allocations during reproduction. Also, some *Daphnia* spp. require relatively higher P and RNA to support maintenance processes than others (Kyle et al., 2006). If *D. lumholtzi* is one of these species, then it would not be advantageous to bet-hedge in a food-limited condition and maintenance should become a priority over ephippium production. This is also supported by

our data, as *D. lumholtzi* in our experiments did not bet-hedge in the low P high Q treatment. The current data also support our previous work (Acharya et al., 2006) showing that the nutrient levels and quantity of the food might affect the extent of ephippium production in *D. lumholtzi*. Previously we showed *D. lumholtzi* grew better on high quality *Scenedesmus* compared to whole and diluted Ohio River seston and at the same time produced more ephippia (compared to two native *Daphnia* species) following the population crash after reaching peak density.

While photoperiod has often been cited as a factor for the induction of diapause, we did not directly measure the effect of photoperiod. Since we were interested primarily in the effects of food quality and quantity, we wanted to eliminate any confounding effects of light level on ephippium production. We found no direct link between different light levels and induction of diapause for *D. lumholtzi*. However, increased population growth at low and ambient light levels may contribute to ephippia production in this species, particularly when food quality and quantity is high. Thus, *D. lumholtzi* might be taking advantage of optimum food conditions to produce resting eggs before conditions deteriorate as a way of hedging their bets (Cáceres & Tessier, 2003).

Our study was conducted using a single clone to avoid any species-specific trait of ephippia production or other genetic variations. Additional studies with wider clone selection would be beneficial before extrapolating our results to all *D. lumholtzi* species. While future studies on the link between food quality and ephippium production for this species (especially with experimental designs that are able to clearly differentiate the effects of food quality and overcrowding) are also needed, our data suggest that *D. lumholtzi* population and ephippium production are related to food quality and quantity, as well as overcrowding. This may in part explain *D. lumholtzi*'s invasion success in North America. If *D. lumholtzi* is using a high level of bet-hedging to ensure survival in deteriorating environments, this provides an abundance of ephippia which can be more easily dispersed than active individuals. Since many invasive aquatic species have the potential to drastically alter the habitats they invade through changes to community and hydrologic structure and nutrient availability (Sea Lamprey, Bullfrog, Giant salvinia, zebra mussels, etc.; Kiesecker & Blaustein, 1997; Strayer et al., 2004;

Wagner et al., 2006), it is vital that we understand what makes invaders successful if we are to predict and manage invasions. *D. lumholtzi* provides a model of successful invasion which we can possibly use to predict the invasion success of future invasive species.

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