LETTER

Phosphorus availability mediates plasticity in life-history traits and predator–prey interactions in *Daphnia*

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Abstract

We analysed growth plasticity of two *Daphnia pulex* clones under low-phosphorus (LP) and high phosphorus (HP) conditions, in the presence of *Chaoborus* kairomones to examine how food quality (P-availability) might impact life-history responses and vulnerability to predation. Overall, clone 1 grew faster, and was larger at maturity. Under HP, both clones responded to kairomones by increasing growth, age and size at maturity, and decreasing fecundity. Under LP, both clones suffered reduced growth, and fecundity. However, the magnitude of response to kairomones depended on a clone by P-availability interaction. *Chaoborus* presented a 1 : 1 clonal mixture under HP or LP, consumed more individuals under LP. Moreover, fewer clone 1 individuals were consumed. Studying the effects of P-availability on life histories, and predator–prey interactions may help us understand the mechanisms generating and maintaining plasticity, as well as influencing genotypic diversity and microevolutionary processes in natural populations.

Keywords

Carbon : phosphorus ratio, clonal selection, ecological stoichiometry, growth rate, phenotypic plasticity.

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INTRODUCTION

Growth rate is an important life-history trait because it is intrinsically linked to and directly affects other life-history traits such as age at maturity, fecundity and optimal body size (among other traits, Arendt 1997), and in turn is affected by numerous biotic and abiotic factors, including resource quantity and/or quality and predation (Stearns 1992). Life-history traits such as growth rate can show considerable plasticity within a single genotype (termed a 'reaction norm'; Falconer 1952) across differing biotic and abiotic conditions (West-Eberhard 2003). Reaction norms of different genotypes have been shown to be directly under selection (Schlichting & Pigliucci 1998). Therefore, plasticity in the growth phenotype of an organism has potentially major fitness consequences.

Theories that predict growth rate trajectories (Arendt 1997) fall mainly into three major categories: (i) competition-based; (ii) predation-based; and (iii) resource availability based. Rapid growth is predicted under high competition because of the competitive advantage that larger individuals

often (but not always) enjoy over smaller-bodied competitors (Brooks & Dodson 1965; Arendt & Wilson 1997). Further, the role of predation in determining growth rates has received considerable attention, as well (Werner & Gilliam 1984). Specifically, the notion of a size-refuge to avoid gape-limited (negative size-selective) predation predicts that rapid growth will be favoured (Spitze 1991; Wellborn 1994). In addition, size-specific predation has been shown to mediate plasticity in life-history traits in a variety of organisms (e.g. snails, Crowl & Covich 1990; *Daphnia*, Spitze 1991). In low resource environments (either low food quantity and/or quality), slow growth will be favoured to reduce the high metabolic cost of growth (Sinervo & Adolph 1994) or to facilitate efficient use of available resources (Chapin 1980).

All these mechanisms are probably at work at any given time, and possibly feedback into one another, ultimately leading to the diversification of prey life-histories (Day *et al.* 2002; Arendt & Reznick 2005). Interspecific diversification is largely preceded by intraspecific (genotypic) variation (Schlichting & Pigliucci 1998). Therefore, to understand

interspecific diversification and plasticity of life-history strategies (i.e. reaction norms) the mechanisms responsible for generating, and maintaining intraspecific diversity/ plasticity in key life-history traits such as growth rate should be studied. Here, we attempt to understand how size-selective predation and resource quality may interact with prey genotypes to produce distinctive life-history responses, and thereby impact fitness differentially. In addition, we explore how differential life-history responses of genotypes under contrasting environmental conditions feedback to the intensity of size-selective predation (i.e. genotype-specific size-selection). We used the parthenogenetic freshwater microcrustacean zooplankter, *Daphnia pulex* (Crustacea: Cladocera) for our investigations.

Much work (e.g. Riessen 1999) has been carried out on life-history shifts of *Daphnia* including work on phenotypic plasticity within (e.g. Lynch *et al.* 1989) and between (Lynch 1980) species. This work has demonstrated that daphniid life-history characters change depending on: food quantity (Lynch *et al.* 1989; Tessier *et al.* 2000), invertebrate predation (Spitze 1985, 1991) and vertebrate predation (Spaak *et al.* 2000). The effects of varying resource quantity on daphniid life-histories are often apparent only under severe food limitation (e.g. < 0.2 mg C L^{-1}; Sterner & Schulz 1998). *Daphnia* that are subjected to negative size-selective predation (i.e. gape-limited invertebrate predators like *Chaoborus*) alter their life-histories by increasing age and size at maturity, and decreasing fecundity (Spitze 1985, 1991). Conversely, under positive size-selective predation (i.e. visually foraging vertebrate predators like fish), daphniids start investing in reproduction earlier and thereby reach maturity earlier, and at a smaller size (Stibor 1992). These opposing life-history shifts are achieved mainly via growth-reproduction tradeoffs, and have been shown to increase fitness (Lynch 1980). Recent studies have highlighted the importance of food quality, particularly the carbon : phosphorus (C : P) ratio of algae, in mediating daphniid life-histories (Sterner 1993; Elser *et al.* 1996). *Daphnia* genotypes feeding on low phosphorus (e.g. C : P *c.* 700) algae exhibit much reduced growth compared with counterparts that feed on high phosphorus algae (e.g. C : P *c.* 150), even when the quantity of food is held constant.

Under conditions favouring rapid growth of prey to avoid predation (i.e. negative size-selective predation), growth-promoting factors such as P-availability may have a large impact on both population genetic structure (Weider *et al.* 2004, 2005a), as well as community dynamics such as predator–prey interactions (MacKay & Elser 1998; Sterner & Elser 2002). Specifically, faster-growing daphniids may have a fitness advantage over slower-growing counterparts because they can reach a size refuge more quickly and reduce predation risk (Hall *et al.* 1976; Lynch 1980). However, in low phosphorus conditions, which retard growth, daphniids may not be able to reach a size refuge fast enough, and may therefore remain vulnerable to invertebrate predators for longer periods of time (MacKay & Elser 1998). Moreover, a genotype that has a greater growth response as reflected in a more 'plastic' reaction norm to both P-availability and predator presence may have a higher probability of survival (i.e. the adaptive plasticity hypothesis; Via & Lande 1985).

Here, we explore how (i) P-availability mediates plasticity in key life-history traits of daphniids; (ii) the magnitude of life-history responses of two genotypes (clones) of *D. pulex* to *Chaoborus* kairomones under P-sufficient (C : P *c.* 150) and P-deficient (C : P *c.* 700) conditions affects the vulnerability of these two genotypes to predation; and (iii) the amount of P-available alters important community parameters like the strength of predator–prey interactions. More specifically, we predict that the genotype which has greater response in key life-history traits like growth rate will enjoy higher survival under *Chaoborus* predation. Furthermore, we predict that under P-sufficient conditions the strength of predator–prey interactions will be muted because of greater numbers of daphniids reaching a size refuge more rapidly. We used the framework of ecological stoichiometry (Sterner & Elser 2002) which makes explicit predictions about the role of P in growth, which can potentially be linked to processes at varying levels of organization (e.g. ribosomal DNA structure, Weider *et al.* 2005b; cellular rate of protein synthesis, Elser *et al.* 1996). In addition, P is often the limiting nutrient in many freshwater systems, and its availability varies greatly among lakes even across small spatial scales (Wetzel 2001). Therefore, its role as an important selective force acting on aquatic populations/genotypes has only recently been examined (Weider *et al.* 2005a). Furthermore, strong P and growth rate couplings have been observed in diverse organisms (Elser *et al.* 2003).

MATERIALS AND METHODS

Life-table experiment

This experiment explored how genotype, and P-availability mediates life-history traits of *D. pulex* cultured in the presence or absence of kairomones of the phantom-midge larvae, *Chaoborus americanus*. Within each predator treatment, there were two levels of genotype (clones 1 and 2) and P-availability (low P and high P). Treatments were replicated six times. Major life-history traits such as, juvenile growth rate (JGR is the rate of change in size from birth to day 5), size at first reproduction (SFR), age at first reproduction (AFR) and fecundity were measured as dependent variables. In addition, neonate size was measured by subsampling five neonates from every clutch of each experimental animal.

Two clones of *D. pulex* (clones 1 and 2) were isolated from a fishless pond (Weider *et al.* 2004) and used for our experiments. We chose these two clones because they were known to exhibit different growth phenotypes (clone 1 generally grew faster than clone 2) and competitive interactions differed between the clones under different levels of P-availability (Weider *et al.* 2005a). Moreover, these clones can be easily identified because they differ at the phosphoglucose isomerase, *Pgi* (EC 5.3.1.9) allozyme locus (Weider *et al.* 2005a). Each clone was established from a single mother under controlled conditions (18 : 6 h light : dark cycle, 20 ± 1 °C). Mothers were kept in 100-mL beakers containing COMBO (Kilham *et al.* 1998) medium, and fed with 1 mg C L^{-1} chemostat-grown *Scenedesmus acutus*. Third clutch neonates (< 24 h old) from fifth-generation mothers were used as experimental animals.

Individual experimental animals were gently transferred onto a depression slide, photographed using a camera fitted to an Olympus$^{®}$ BX51 compound microscope (Olympus America Inc., Melville, NY, USA), measured at 36 × screen magnification (1200 × 1600 dpi resolution), and introduced into separate 100-mL glass jars in media containing phantom-midge larvae (*C. americanus*) kairomones. Daphniids have been shown to alter their life-histories in the presence of predator kairomones (Tollrian & Dodson 1999). *Chaoborus* kairomones were generated by incubating five fourth instar larvae in each of six, 1 L glass jars containing COMBO medium. Each jar was fed 30 *D. pulex* (1 : 1 mixture of the two clones) every 12 h. Predator incubations were conducted at 20 ± 1 °C in total darkness. Predator-conditioned media from six jars were pooled and filtered using GF/F filters (4.25-cm diameter; 0.7 µM; Whatman International Ltd, Maidstone, England), and used in experimental beakers. Consumers are also capable of excreting P into the environment (Vanni 2002), therefore, total P content (APHA 1992) of both predator-conditioned and unconditioned media was determined on weekly samples. We found no significant difference in total P content between the two media (predator-conditioned, 54.45 ± 0.48 µmol L^{-1}; unconditioned, 54.09 ± 0.82 µmol L^{-1}; $n = 4$, paired-$t = 0.68$, $P = 0.54$).

Experimental animals in predator-conditioned medium were fed either high phosphorus (HP, molar C : P = 140), or low phosphorus (LP, molar C : P = 750) *S. acutus*, at a concentration of 1 mg C L^{-1} day^{-1}. The experiment ended when the experimental animals reached their fifth adult moult. During the course of the experiment, growth rate and reproductive condition of animals were monitored daily using a microscope at 5 × magnification to the nearest 0.02 mm. In addition, all animals were photographed every 7 days and measured at 36 × screen magnification (see above). Predator-conditioned media and algal food were changed daily to ensure constant kairomone and food

concentration throughout the experiment. A similar life-table experiment using bluegill sunfish (*Lepomis macrochirus*) kairomones was also conducted and these results are to be published elsewhere (P.D. Jeyasingh, in preparation).

Direct predation experiment

To understand whether P-availability altered predation intensity, 40 < 6 h-old-neonates (1 : 1 clonal mixture of clones 1 and 2) were offered to similarly-sized, individual fourth instar *C. americanus* (size, 9.6 ± 0.3 mm) under P-sufficient (HP, $n = 16$) or P-deficient (LP, $n = 16$) conditions. Twenty neonates from each clone were photographed immediately before the start of the experiment to estimate initial size differences between the two clones and two phosphorus treatments. The number of neonates consumed after 48 h in HP and LP treatments was compared using a Student's *t*-test. The number of clones 1 and 2 individuals remaining at the end of the experiment was determined by allozyme screening of the *Pgi* locus (Hebert & Beaton 1993). The proportions of clones 1 and 2 remaining were compared using McNemar's test for equal proportions (McNemar 1947; *Proc Freq option McNem*, SAS Online Doc$^{®}$, SAS Institute 2000). Two jars per P-treatment were stocked with 40 neonates (1 : 1 clonal mixture) in the absence of *C. americanus* larvae to determine background mortality rates. Two neonates remaining from each of the experimental jars and 10 neonates from each of the control jars were photographed prior to running allozymes for determining final size differences between the two clones under the different treatments. Finally, the size of each *Chaoborus* larva was measured under a dissecting microscope (to the nearest 0.02 mm at 5 ×) after the experiment was concluded.

All statistical tests were performed at $\alpha = 0.05$, using SAS$^{®}$ software (SAS Institute 2000). Multiple-comparisons of least square mean values of life-history traits among different treatments were performed at $\alpha = 0.001$, after correcting for table-wide error using a Bonferroni correction (Rice 1989).

RESULTS

P-availability effects on major life-history traits

Overall, both clones responded to *Chaoborus* kairomones as predicted by life-history theory (Fig. 1). Moreover, P-availability had a significant effect on major life-history traits (Fig. 1). Results from the ANOVA on JGR yielded significant higher order interactions (Table 1). Graphical analysis of the interactions indicated that JGR of daphniids feeding on HP algae was much higher than those feeding on LP algae (Fig. 2a,b). Moreover, daphniids in the presence of *Chaoborus* kairomones grew at a slightly higher rate
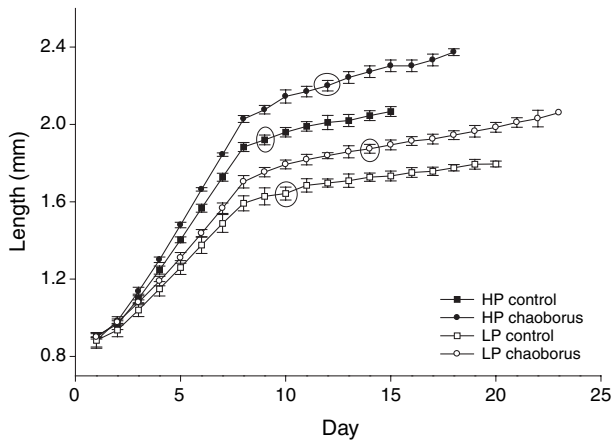
Figure 1 Clone 1 growth curve for *Chaoborus* treated animals and controls under high phosphorus and low phosphorus conditions. Data points indicate mean ± 1 SE of body length in mm for each day of observation. Circles indicate approximate age at first reproduction (AFR, *x*-axis) and size at first reproduction (SFR, *y*-axis) (clone 2 exhibited similar growth curves for these treatments as well; data not shown).

compared with control animals (Fig. 2a,b). However, the magnitude of JGR response to *Chaoborus* kairomones appears to be clone-specific, as well as specific to P treatment. The response of clone 1 was greater under LP conditions compared with HP conditions (Fig. 2a inset).

Conversely, the response of clone 2 was greater in HP conditions compared with its response under LP conditions (Fig. 2b inset).

Heterogeneity in JGR most probably contributed to similar higher order interactions in the SFR ANOVA (Table 1). Least square mean values interaction plots of SFR indicate similar trends as seen for JGR. Animals feeding on HP algae were much larger at first reproduction compared with counterparts feeding on LP algae (Fig. 3a,b). Also, all experimental animals responded to the presence of *Chaoborus* kairomones by increasing their SFR (Fig. 3a,b), although the degree of response varied between clones depending on P-availability. The difference in SFR of clone 1 grown in the presence or absence of *Chaoborus* kairomones is greater under LP conditions compared with HP conditions (Fig. 3a inset). On the contrary, the difference in SFR of clone 2 grown in the presence or absence of kairomones was greater under HP conditions (Fig. 3b inset).

Age at first reproduction was significantly affected by treatment effects (Table 1). Tukey's HSD *post hoc* analyses indicated that AFR was greater for animals in the *Chaoborus* treatment. Animals under LP conditions also matured at an older age compared with those feeding on HP algae. However, the two clones did not differ in their AFR within the predator and nutrient treatments.

Results of the ANOVA on fecundity was also confounded by significant higher order interactions (Table 1). Further

Table 1 Summary of differences in type III least square mean values of life-history traits because of clone (genotype), phosphorus (P) treatment, predator treatment and their interactions – *P*-values of three-way ANOVA

Trait	Clone	P-treatment	Predator treatment	P × clone interaction	Clone × predator interaction	P × predator interaction	P × predator × clone interaction
JGR	< 0.0001	< 0.0001	< 0.0001	0.0257	0.8151	0.4225	**0.0003**
SFR	< 0.0001	< 0.0001	< 0.0001	0.1141	0.8189	0.0410	**< 0.0001**
AFR	0.1405	**< 0.0001**	**< 0.0001**	0.1523	0.4105	0.0812	0.5772
Fecundity	< 0.0001	< 0.0001	< 0.0001	**< 0.0001**	0.1707	**0.0003**	0.0376
Neonate size	0.0128	**< 0.0001**	**< 0.0001**	0.0847	0.9547	0.0963	0.4716

JGR, juvenile growth rate; SFR, size at first reproduction; AFR, age at first reproduction.
Table-wide error correction; $\alpha = 0.05/35 = 0.001$. Significant parameters are represented in bold.
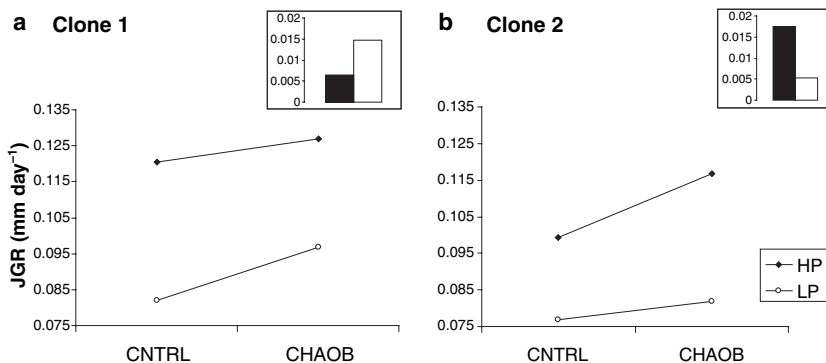

Figure 2 Least square mean values of juvenile growth rate (JGR) for clones 1 and 2 grown in high phosphorus (HP, –◆–) or low phosphorus (LP, –○–) conditions in the absence of kairomones (CNTRL) or in the presence of *Chaoborus* kairomones (CHAOB). The magnitude of response to kairomones under HP (closed bars) and LP (open bars) conditions are shown in the inset.

a Clone 1

b Clone 2

Figure 3 Least square mean values of size at first reproduction (SFR) for clones 1 and 2 grown in high phosphorus (HP, –◆–) or low phosphorus (LP, –○–) conditions in the absence of kairomones (CNTRL) or in the presence of *Chaoborus* kairomones (CHAOB). The magnitude of response to kairomones under HP (closed bars) and LP (open bars) conditions are shown in the inset.
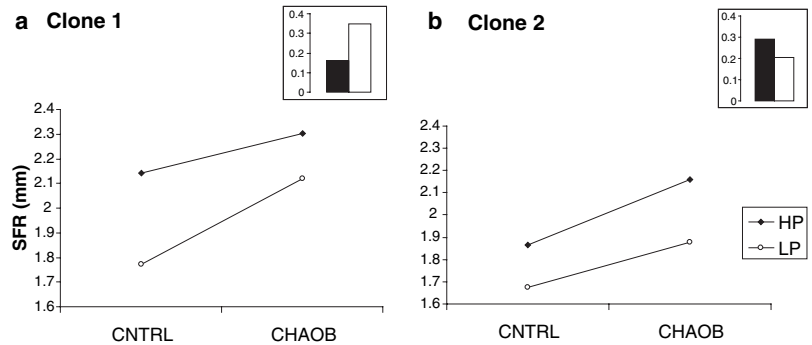
analyses indicated that both clones had higher fecundity in HP treatments compared with LP treatments (Fig. 4). Moreover, fecundity was reduced for both clones in the presence of *Chaoborus* kairomones compared with control conditions, in both HP and LP treatments (Fig. 4). The magnitude of fecundity response to the presence of *Chaoborus* kairomones by clone 1 appears to be independent of P-availability (Fig. 4). However, clone 2 shows a more pronounced reduction in fecundity in the presence of *Chaoborus* kairomones under HP conditions (Fig. 4). Interactions may also have arisen because of the fact that both clones suffered large reductions in fecundity under LP conditions and had nearly identical fecundities among LP predator treatments, but differed significantly among predator treatments under HP conditions.

Overall ANOVA on the size of neonates born to experimental animals indicated significant treatment effects (Table 1). *Post hoc* analysis revealed that the size of neonates born to mothers cultured in HP conditions was significantly larger than those born to mothers cultured in LP conditions for both clones. Moreover, mothers treated with *Chaoborus* kairomones gave birth to significantly larger neonates compared with mothers exposed to no kairomones (con-
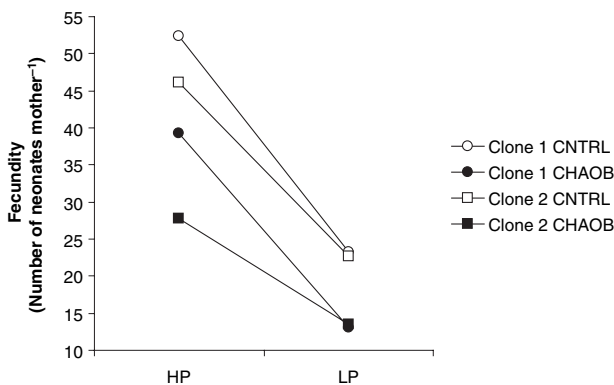
trols). Finally, clone 1 mothers gave birth to significantly larger neonates compared with clone 2 under all treatments.

Effects of P-availability on predator–prey interaction strength

There were no differences in the initial neonate body sizes between the two clones (clone 1, 0.69 ± 0.03 mm; clone 2, 0.69 ± 0.04 mm; $n = 20$, $t = 0.19$, $P = 0.85$). Likewise, the size of *Chaoborus* larvae in the LP and HP treatments were not significantly different (LP, 9.6 ± 0.3 mm; HP, 9.5 ± 0.3 mm; $n = 16$, $t = -0.94$, $P = 0.35$). However, significantly fewer daphniids were consumed by *Chaoborus* larvae in the HP treatments compared with the LP treatments ($n = 16$, $t = 28.5$, $P < 0.0001$). Out of the 40 neonates offered, *c.* 49% (19.75 ± 2.29) were consumed under LP conditions compared with only *c.* 34% (13.71 ± 3.98) in the HP conditions (Fig. 5a). There was negligible mortality $< 4\%$ (1.75 ± 0.95) in control jars (without *Chaoborus* larvae) (Fig. 5a). McNemar's test performed on the entire data (both LP and HP treatments) indicated significantly fewer clone 1 individuals were consumed ($n = 30$, $\chi^2 = 30.53$, $P < 0.0001$) (Fig. 5b,c). When the proportion of clones 1 and 2 consumed were compared within treatments, significantly fewer clone 1 individuals were consumed in each treatment (Fig. 5b – LP, $n = 16$, $\chi^2 = 19.87$, $P < 0.0001$; Fig. 5c – HP, $n = 14$, $\chi^2 = 10.68$, $P = 0.001$). Final neonate sizes were significantly larger in the HP treatment compared with the LP treatment (HP, 1.4 ± 0.13 mm; LP, 0.92 ± 0.05 mm; $n = 20$, $t = 13.74$, $P < 0.0001$). However, final neonate sizes were not significantly different between the two clones within the LP (clone 1, 0.92 ± 0.06 mm; clone 2, 0.92 ± 0.06 mm; $n = 20$, $t = -0.36$, $P = 0.72$) or the HP treatments (clone 1, 1.45 ± 0.05 mm; clone 2, 1.39 ± 0.13 mm; $n = 20$, $t = -0.33$, $P = 0.74$).

Figure 4 Least square mean values for fecundity of both clones (○, clone 1; □, clone 2) in the absence (open symbols) or presence (closed symbols) of *Chaoborus* kairomones under high phosphorus and low phosphorus conditions.

DISCUSSION

Our results clearly demonstrate that P-availability affects life-history traits of daphniids by its strong positive effect on
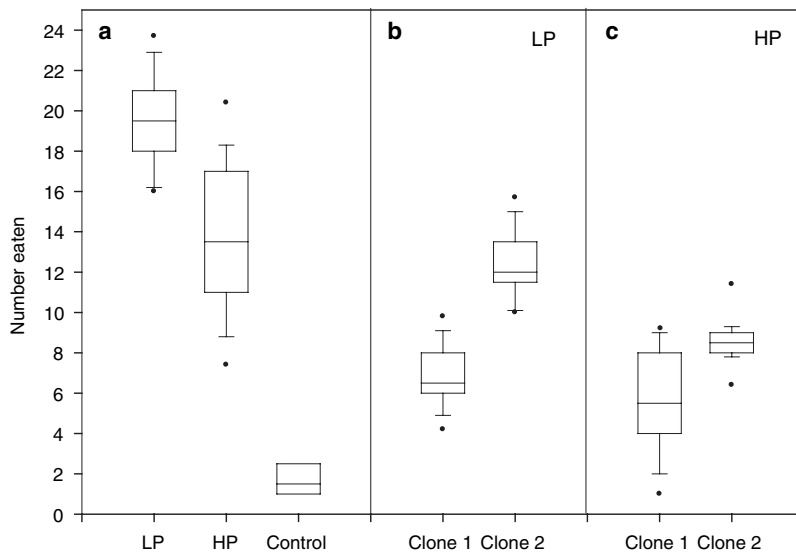
Figure 5 (a) Box plots comparing number of daphniids consumed by *Chaoborus* in low phosphorus (LP), high phosphorus (HP) treatments, control denotes no predator. (b) Number of clones 1 and 2 individuals consumed after 48 h in LP treatment. (c) Number of clones 1 and 2 individuals consumed in HP treatment. The boundary of the box closest to zero indicates the 25th percentile, the line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers indicate the 10th and 90th percentiles of a box plot. Above and below the box indicates the 90th and 10th percentiles respectively. Clones 1 and 2 were genotyped using allozyme markers.

growth rate, and therefore can have considerable evolutionary and ecological significance. Results indicate that genotypes capable of faster growth are at a selective advantage (i.e. lower vulnerability) under negative size-selective predation, and P-availability magnifies this effect. In addition, we found that the magnitude of response in life-history traits to predator kairomones is genotype-specific, and depends on P-availability. Therefore, P-availability may play a major role in mediating shifts in population genetic structure leading to microevolutionary changes. Finally, we found that the intensity of predation on daphniids by *Chaoborus* was much lower under P-sufficient conditions, indicating that P-availability can alter predator–prey interaction strengths leading to changes in community structure.

Previous work on these two clones (Weider *et al*. 2005a) has demonstrated clonal differences in competitive abilities under high-P (fertilized) and low-P (unfertilized) conditions. Clone 1 excluded clone 2 in competition experiments under high-P conditions. Conversely, slower growing clone 2 outcompeted clone 1 under low-P conditions. Results from the current study suggest that clone 2 may have lower fitness under *Chaoborus* predation regardless of the nutrient (food) environment. Therefore, one might predict that clone 2 would have been at a competitive disadvantage in the shallow, fishless pond in northwestern Iowa from which they were isolated (Weider *et al*. 2004). However, closer examination of the interactions revealed that the degree of plasticity in key life-history phenotypes (Figs 2 and 3) may facilitate clonal coexistence by increasing each clone's probability of survival. Although clone 1 may enjoy higher overall survival under *Chaoborus* predation and under HP conditions, clone 2, may increase its mean survival probability by exhibiting a greater response to *Chaoborus* (Figs 2 and 3), compared with clone 1. On the contrary,

under LP conditions and *Chaoborus* predation, clone 1 may increase its mean survival probability compared with clone 2, because it exhibited a greater response in JGR compared with clone 2 (Fig. 2a,b insets). These results indicate that when faced with unfavourable competitive conditions, the degree of phenotypic response of genotypes to predators may be greater, and thereby increase their survival probability. However, the relative importance of the degree of plasticity of a trait, and the absolute value of the trait remains to be ascertained.

Genotype-specific morphological and behavioural responses to predators have been observed in daphniids before (Tollrian & Harvell 1999). Final neonate sizes after 48 h of *Chaoborus* predation did not differ between the two clones. We believe that this may be due to the role of *Chaoborus* in altering size-structure. *Chaoborus* larvae consumed more clone 2 individuals (Fig. 5); however, the remaining clone 2 individuals may have been larger than those consumed, thereby obscuring any absolute size differences found in the life-history experiment (where clone 2 was always smaller; e.g. see Fig. 3). Although we did not find any evidence for morphological differences between these two genotypes, different behavioural responses (e.g. dial vertical migration; Weider 1984; De Meester 1993) may help explain some of the variance in mortality between the genotypes, and warrants further investigation. Furthermore, behavioural differences may also require differential allocation of materials resulting in life-history trade-offs (De Meester *et al*. 1995) that could vary differentially between the two clones.

Results presented here suggest that in addition to incurring a severe growth penalty (Fig. 1) under P-limitation, daphniids may also suffer increased predation by invertebrate predators (Fig. 5), potentially altering per-capita

predator–prey interaction strengths. The magnitude of *Chaoborus* predation on daphniids is highly variable among lakes. In some lakes, *Chaoborus* are known to reduce daphniid populations significantly, while in other cases they have negligible effects on *Daphnia* (Elser *et al.* 1987). MacKay & Elser (1998) hypothesized that these discrepancies in predator-prey interaction strengths among lakes may be due to P-limitation of daphniid growth. To test this hypothesis, they used seston from lakes naturally differing in their C : P signature, and therefore may have differences in species composition, size structure and biochemical composition (MacKay & Elser 1998). In the present study, even though we used chemostat-grown *Scenedesmus* algae in both experiments, our results are still consistent with those found by MacKay & Elser (1998). Results from the present study also indicate that individual daphniids actually increased their JGR when exposed to *Chaoborus* kairomones, suggesting that under *Chaoborus* predation, daphniids may become more P-sensitive. Furthermore, the amount of P available to daphniids may play a role in mediating predator–prey interaction strengths, as indicated by the results of the direct-predation experiment. In addition, *Daphnia* are considered keystone grazers in ponds and lakes. Therefore, large differences in the magnitude of invertebrate predation on daphniids because of P-availability in the environment could affect transfer efficiency of energy and nutrients to higher trophic levels (Sterner & Elser 2002).

Several physico-chemical parameters (e.g. temperature and dissolved oxygen) have been shown to alter genetic structure of daphniid populations (Weider & Lampert 1985; Weider 1985). Results from the present study suggest that nutrient (phosphorus) availability may also alter clonal structure of daphniid populations. Moreover, fitness of certain genotypes (clones) may be affected more severely under *Chaoborus* predation and P-limitation. Although a causal link between P-availability, clone-specific growth rate and clone-specific predation rate, could not be verified in the same experiment, results (Fig. 5) suggest that under P-limited conditions the magnitude of predation and directional clonal selection on *Daphnia* populations by *Chaoborus* may be high. The underlying mechanism for increased selection pressure on daphniids may be due to the significant role phosphorus plays in affecting daphniid growth (Elser *et al.* 1996). Individuals may be in the vulnerable size range to *Chaoborus* predation for longer periods because of retarded growth. Numerous studies (see Lynch 1984) have observed that the density and genotypic diversity of lake cladoceran populations are extremely vulnerable to changes in predation and nutrient regimes. It could be possible that both predators and nutrients interact to regulate cladoceran densities as well as genotypic diversity by affecting the degree of plasticity in key life-history traits such as growth rate.

Our study demonstrates that key macronutrients like phosphorus can mediate plasticity in life-history traits even within a single genotype. The degree of plasticity is genotype-specific with significant evolutionary implications in light of size-selective predation. Utilizing the framework of ecological stoichiometry (Sterner & Elser 2002) may provide us with a robust understanding of the eco-evolutionary mechanisms operating at different levels of organization (i.e. intra-individual to ecosystem level) that may generate divergence and plasticity in life-history strategies. Such plastic life-history responses may in turn play a major role in the maintenance of genetic variation in natural populations.

ACKNOWLEDGEMENTS

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