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Predator-induced phenotypic plasticity in the exotic cladoceran *Daphnia lumholtzi*

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SUMMARY

1. The exotic cladoceran *Daphnia lumholtzi* has recently invaded freshwater systems throughout the United States. *Daphnia lumholtzi* possesses extravagant head spines that are longer than those found on any other North American *Daphnia*. These spines are effective at reducing predation from many of the predators that are native to newly invaded habitats; however, they are plastic both in nature and in laboratory cultures. The purpose of this experiment was to better understand what environmental cues induce and maintain these effective predator-deterrent spines. We conducted life-table experiments on individual *D. lumholtzi* grown in water conditioned with an invertebrate insect predator, *Chaoborus punctipennis*, and water conditioned with a vertebrate fish predator, *Lepomis macrochirus*.
2. *Daphnia lumholtzi* exhibited morphological plasticity in response to kairomones released by both predators. However, direct exposure to predator kairomones during postembryonic development did not induce long spines in *D. lumholtzi*. In contrast, neonates produced from individuals exposed to *Lepomis* kairomones had significantly longer head and tail spines than neonates produced from control and *Chaoborus* individuals. These results suggest that there may be a maternal, or pre-embryonic, effect of kairomone exposure on spine development in *D. lumholtzi*.
3. Independent of these morphological shifts, *D. lumholtzi* also exhibited plasticity in life history characteristics in response to predator kairomones. For example, *D. lumholtzi* exhibited delayed reproduction in response to *Chaoborus* kairomones, and significantly more individuals produced resting eggs, or ephippia, in the presence of *Lepomis* kairomones.

Keywords: biological invasions, *Daphnia lumholtzi*, ephippia, kairomones, phenotypic plasticity

Introduction

The establishment of a non-native species is, in part, determined by its ability to adapt to the abiotic and biotic characteristics of an invaded habitat (Crawley, 1986; Moyle & Light, 1996; Miller, Kneitel & Burns, 2002). However, local environmental conditions often vary within a given habitat and phenotypes that increase survival and fitness under one set of conditions may not increase survival and fitness under a different set of habitat conditions. Phenotypic plasticity, the ability of a genotype to produce different phenotypes in response to varying environmental conditions, may therefore be an important

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attribute contributing to the successful colonisation of non-native habitats (Barrett & Richardson, 1986; Lodge, 1993).

One biotic factor that varies in planktonic ecosystems and is also an important factor influencing the success of potential invaders is predation (Crawley, 1986; Miller *et al.*, 2002). In freshwater plankton communities predation pressures vary spatially and temporally both within and between habitats. Invertebrate and vertebrate predators commonly prey upon zooplankton, and both types of predators exhibit significant differences in selectivity based on prey size (Dodson, 1974; Zaret, 1980). As a result, size-selective predation has played a major role in the evolution of plankton morphology, life history, and behaviour (see review by Tollrian & Dodson, 1999).

Many planktonic taxa, including algae (Lampert, Rothhaupt & von Elert, 1994), ciliates (Kusch, 1993), rotifers (Stemberger & Gilbert, 1987), and cladocerans (Tollrian & Dodson, 1999) exhibit a high degree of phenotypic plasticity in response to water-borne chemical cues, or kairomones, that are released by predators. Kairomones are predator-specific, and allow zooplankton to detect potential predators first, and then to allocate energy differentially towards morphology, growth, and reproduction to reduce immediate predation risks (Tollrian & Dodson, 1999).

A large body of research has shown that several species of the genus *Daphnia* produce elaborate morphological structures including spines, neckteeth, and helmets in response to kairomones released by invertebrate predators (e.g. Krueger & Dodson, 1981; Tollrian, 1995). Because invertebrate predators are usually only slightly larger than their prey, small differences in prey shape and size can significantly alter their vulnerability to predation (O'Brien, Kettle & Riessen, 1979; Havel, 1985). In contrast, visually feeding planktivorous fish are generally much larger than their prey and their gape size is large enough to ingest most zooplankton without difficulty (O'Brien, 1987). Thus, a reduction in body size is commonly an effective defence for visual predation (O'Brien, 1987).

Reproductive costs are often associated with the expression of morphological defences in *Daphnia* (O'Brien *et al.*, 1980; Havel & Dodson, 1987). However, studies designed to examine these costs have produced mixed results. For example, comparative studies of predator-induced spined morphs of *Daphnia pulex* have shown a decrease, an increase, or no change in fitness relative to non-spined morphs (see Tollrian, 1995). In addition, kairomone-induced life history shifts occur independent of induced morphological defences and further increase fitness (Dorazio & Lehman, 1983; Taylor & Gabriel, 1992).

The exotic cladoceran *D. lumholtzi* (Sars), which has recently invaded freshwater systems throughout the United States (Sorenson & Sterner, 1992; Havel, Mabee & Jones, 1995; Muzinic, 2000), possesses head and tail spines longer than those found on any other North American *Daphnia* (Havel & Hebert, 1993; Tollrian & Dodson, 1999). Unlike the less extreme morphological defences of native *Daphnia*, the exuberant spines of *D. lumholtzi* are long enough to create handling difficulties even for small vertebrate fish predators (Swaffar & O'Brien, 1996). While it is clear that the spines of *D. lumholtzi* are effective at reducing predation, these structures are highly plastic. For example, spine lengths vary seasonally (Sorenson & Sterner, 1992), become greatly reduced in long-term laboratory cultures (Havel & Hebert, 1993), and long spines can be induced by exposing individuals to elevated temperatures (Yurista, 2000).

We conducted life-table experiments with laboratory-cultured *D. lumholtzi* in water conditioned with kairomones from either of two common planktivores: the invertebrate predator *Chaoborus punctipennis*, and the vertebrate predator *Lepomis macrochirus*. We addressed several questions in this study: (1) Does the presence of invertebrate and vertebrate predator kairomones induce predator-specific morphological changes in *D. lumholtzi*? If so (2) are there reproductive costs associated with the expression of long spines in individual *D. lumholtzi*? Or (3) does *D. lumholtzi* exhibit predator-induced life history alterations independent of spine formation?

Methods

Cultures

The *D. lumholtzi* clone used in this experiment was originally obtained from Clinton Reservoir in August 1997. This large reservoir is located 3 km west of Lawrence, KS, and was invaded by *D. lumholtzi* before 1994 (Dzialowski, O'Brien & Swaffar, 2000). Prior to the start of the experiment, *D. lumholtzi* were maintained in laboratory stock culture for several months, during which time their spine lengths became greatly

reduced. The lake water used throughout the experiment was obtained from Cross Reservoir, located 4 km north of the University of Kansas at the University of Kansas Field Station and Reserves (KSR). All *Chaoborus*, *Lepomis*, and zooplankton used to develop and maintain predator cultures were also collected from this small reservoir, which has not yet been invaded by *D. lumholtzi*.

To initiate the start of the life-table experiments, we inoculated individual *D. lumholtzi* from the stock cultures into each of 15 separate tissue culture flasks containing 50 mL of (0.45 μm membrane-filtered) lake water. These individuals were transferred to fresh membrane-filtered lake water every other day, and fed equal concentrations of *Selenastrum* sp. and *Chlamydomonas reinhardii* at final flask concentrations of 10^5 cells mL^{-1}. The organisms were cultured under these conditions for two generations, at which time all day 0 neonates were pooled. These neonates provided the founding organisms for the life-table experiments below.

Life-table experiments

Life-table experiments were conducted on individual day 0 neonates that were grown in each of two predator-conditioned treatments, and in a non-predator treatment that served as a control. Predator-conditioned media was prepared using techniques similar to those reported elsewhere (Weider & Pijanowska, 1993; Repka & Walls, 1998). Three aquaria (40 L) were filled with lake water that was first screened (38 μm) and then autoclaved to eliminate any remaining organisms. We added eight small (3–10 cm) *L. macrochirus* to the first aquarium (0.2 individuals L^{-1}; Sakwinska, 2002); 400 fourth instar *C. punctipennis* larva to the second aquarium (10 individuals L^{-1}; Black & Dodson, 1990; Luning, 1992); and nothing was added to the third aquarium (control). Predators were fed zooplankton weekly to ensure that predator starvation did not diminish the level of kairomone being produced (Krueger & Dodson, 1981; Havel, 1985). In addition, *Chaoborus* larvae were added to the *Chaoborus* conditioning tank throughout the course of the experiment to account for losses caused by emergence.

To begin the life-table experiments we filtered (0.45 μm) 2 L of water from each of the three conditioning tanks, and then filled 15 culture flasks with *Lepomis*-conditioned water, 15 with *Chaoborus*-conditioned water, and 15 with non-conditioned control water. One day 0 neonate, from the stock cultures described above, was then added to each of the 45 flasks. Organisms were transferred daily into clean tissue culture flasks containing fresh conditioned water, and re-supplied with equal volumes of *Selenastrum* spp. and *C. reinhardii* at a final total cell concentration of 10^5 cells mL^{-1} in each tissue culture flask. Flasks containing animals were housed in an incubator (16 : 8 L/D cycle) at 25 ± 1 C which is within the optimum temperature of *D. lumholtzi* (Lennon, Smith & Williams, 2001). We added filtered (38 μm), autoclaved lake water to each conditioning tank daily in order to replace the water that was removed.

At each daily transfer we recorded survivorship, fecundity, and the presence or absence of ephippia. Every third day, starting on day 0, we also measured head spine (HS), tail spine (TS), and core body (CB) lengths of experimental individuals (Fig. 1) with an

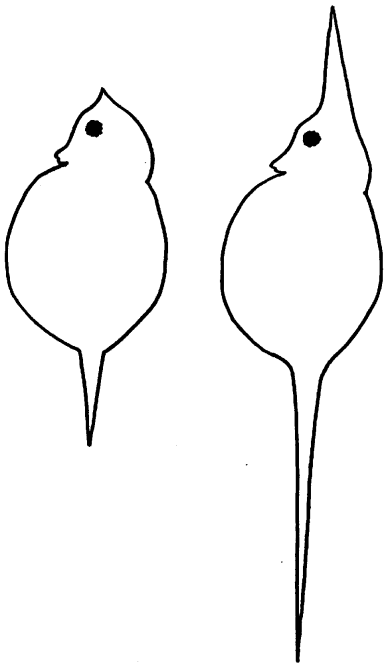

Fig. 1 *Daphnia lumholtzi* from laboratory cultures (left) and natural populations (right). Head spine (HS) was measured from the top of the spine to the top of the eye; core body (CB) was measured from the top of the eye to the base of the tail; and tail spine (TS) was measured from the base of the tail to the end of the tail.

M-5 Wild dissecting microscope (Wild, Switzerland). Length measurements were taken through day 21, and life-table experiments were continued until all of the founding organisms died. In addition, all newborn neonates were removed from the tissue culture flasks and counted from each treatment daily. The spine and body lengths of first clutch neonates were measured in order to determine if there was a maternal, or pre-embryonic effect of kairomone exposure on *D. lumholtzi* spine lengths. No distinction was made between male and female neonates when they were counted each day; therefore, both were included in the analysis of all reproductive measures described below.

The intrinsic rate of increase [r (day^{-1})] was calculated for *D. lumholtzi* for each of the three treatments using Euler's equation:

$$l = \sum e^{-rx} l(x) b(x)$$

where x is the age (days), $l(x)$ the age-specific survivorship, and $b(x)$ the age-specific fecundity (Gotelli, 2000). Jack-knife methods were used to obtain replicate r-values for statistical analysis (Meyer *et al.*, 1986). Survivorship and fecundity values were also used to determine: the age at first reproduction (the day in which the first clutch was released from the brood chamber); the net reproductive rate (R_0, total number of offspring produced in an organism's lifetime, for individuals that produced at least two clutches); and the mean clutch size for individuals in each treatment.

Statistical analysis

An unbalanced multivariate repeated measures ANOVA (RM-ANOVA; SAS v8.0) was used to test for significant differences in the spine and body lengths (HS, TS, CB) of the individuals grown in the different predator-conditioned treatments throughout the course of the experiment. An unbalanced RM-ANOVA was necessary because individual *D. lumholtzi* died throughout the course of the experiment. Tukey's honestly significantly different (HSD) *post hoc* test ($P < 0.05$) was used to compare individual treatments (Sokal & Rohlf, 1995). Spine and body lengths for the experimental individuals are presented as the least square mean ± SEM. We used one-way ANOVA to test for differences in spine and body lengths of the first clutch neonates.

Differences in the intrinsic rate of growth, net reproductive rate, and mean clutch size between treatments were determined using one-way ANOVA. One response variable did not meet the assumptions for parametric analysis (age at first reproduction), in which case we used a non-parametric Kruskall–Wallis test to determine if there were between-treatment differences. Dunn's pairwise comparison ($P < 0.05$) was then used to compare significantly different treatment mean values (Rosner, 1986). All life history data are reported as mean ± SEM unless noted otherwise.

We used Fisherex (N. Slade, University of Kansas) to test for differences in ephippia production (percentage of individuals producing ephippia) between treatments. Fisherex is an extension of Fisher's exact test (Sokal & Rohlf, 1995) that produces a single P-value based on multiple column contingency tables with small sample sizes.

Results

Morphological responses

RM-ANOVA revealed that there were significant effects of kairomone exposure on tail spine ($P = 0.002$, $F_{2,42} = 10.31$) and core body ($P < 0.0001$, $F_{2,42} = 32.43$) lengths. Overall, individuals grown in the *Chaoborus* treatment had significantly smaller TS, and CB lengths than individuals grown in both the control and *Lepomis* treatments (Tukey's HSD). In contrast, there were no significant treatment differences between individuals in the control and *Lepomis* treatments with respect to these two measurements (Tukey's HSD). On day 3 however, *D. lumholtzi* grown in the *Lepomis*-conditioned water had significantly smaller TS and CB lengths than individuals grown under control conditions (ANOVA, $P < 0.05$). Beyond day 3, individuals grown in the *Lepomis* treatment were not significantly different from the control individuals. There was no significant effects of kairomone exposure on head spine length (RM-ANOVA; $P = 0.52$, $F_{2,42} = 0.67$).

Several morphological differences were also observed in neonates produced from *D. lumholtzi* grown in the *Lepomis* treatment. For example, these neonates had significantly larger HS (ANOVA, $P < 0.001$) and TS (ANOVA, $P < 0.001$) lengths than neonates produced from control and *Chaoborus* individuals (Fig. 2). In addition, the average CB length of neonates produced

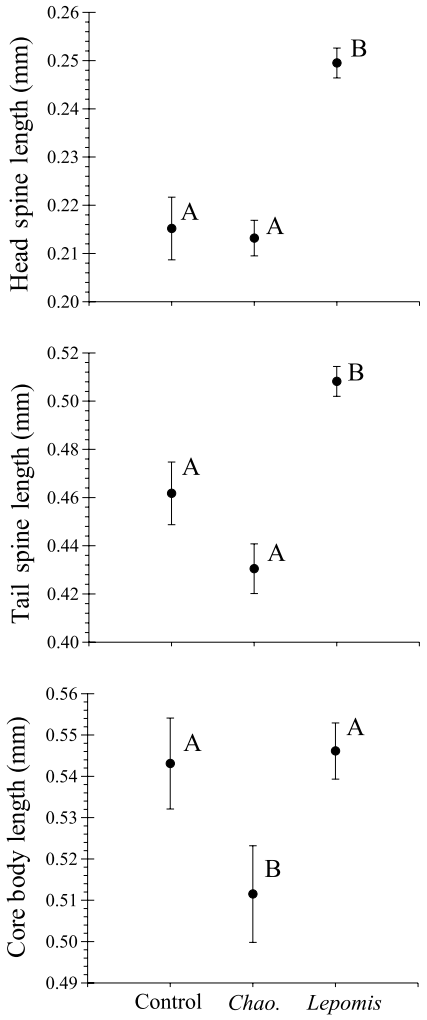

Fig. 2 Spine and body length measurements of first clutch neonates produced from individual *D. lumholtzi* grown in control ($n = 45$), *Chaoborus*- ($n = 42$) and *Lepomis*-conditioned ($n = 72$) water. Error bars represent SEM; significant differences in mean values are represented by different letters.

from individuals grown in the *Chaoborus* treatment was significantly smaller (ANOVA, $P < 0.001$) than the average CB length of neonates produced in the *Lepomis* and control treatments (Fig. 2).

Life history responses

Most of the reproductive measures used in this study were greatest for individuals grown in the *Lepomis* treatment (Table 1). For example, the intrinsic rate of increase (r) of individuals grown in the *Lepomis* treatment (0.43 ± 0.018 day^{-1}) was significantly larger (ANOVA, $P = 0.005$) than the r-value for individuals grown in *Chaoborus* treatment (0.27 ± 0.019 day^{-1}). Similarly, individuals from the *Lepomis* treatment had higher r-values than control individuals (0.35 ± 0.047 day^{-1}), although these results were not significant. In addition, there was no significant difference between control *Daphnia* and those from the *Chaoborus* treatment (Table 1).

The age at first reproduction was significantly delayed (Kruskall–Wallace, $P < 0.001$) for individuals grown in the *Chaoborus* treatment when compared with individuals grown in both the *Lepomis* and control treatments (Table 1). The median age at first reproduction for individuals grown in the *Chaoborus* treatment was day 9.0 ± 0.42 compared with day 5.0 ± 0.10 for control individuals and day 6.0 ± 0.22 for individuals grown in the *Lepomis* treatment (Table 1).

The net reproductive rate (R_0) of *D. lumholtzi* grown in the *Lepomis* treatment was significantly higher (ANOVA, $P = 0.025$) than the R_0 of individuals grown in the *Chaoborus* treatment (Table 1). There was, however, no significant difference between the R_0 in the control and *Chaoborus* treatments. On average,

Table 1 Comparisons of life history characteristics of *D. lumholtzi* grown in control, *Chaoborus* and *Lepomis*-conditioned water

Treatment	Intrinsic rate of increase (r) (day^{-1})	Age at first reproduction (days)	R_0 (neonates per female)	Mean clutch size
Control	0.353 (0.047; 15) AB	5 (0.10; 11) A	45.8 (11.0; 6) AB	6.8 (0.98; 6) A
Chaoborus	0.274 (0.019; 15) A	9 (0.42; 13) B	43.4 (7.47; 10) A	9.6 (0.93; 10) B
Lepomis	0.432 (0.018; 15) B	6 (0.22; 15) A	72.0 (7.21; 14) B	10.7 (0.47; 14) B
P-value	0.005	<0.001	0.025	0.004

All reported values are mean, except for age at first reproduction, which is the median. Standard error and sample size are represented in parentheses.
Significant differences in mean values are represented by different letters.
Between treatment differences for intrinsic rate of growth, net reproduction, and mean clutch size were determined using one-way ANOVA.
Differences in age at first reproduction were determined using a Kruskall–Wallis test.

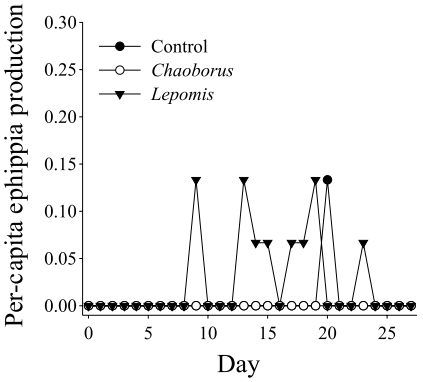

Fig. 3 Timing of ephippia production in *D. lumholtzi* grown in control, *Chaoborus*- and *Lepomis*-conditioned water. Note that individuals grown in the *Chaoborus*-conditioned water produced no ephippia.

individuals grown in the *Lepomis* treatment produced 72.0 ± 7.21 neonates compared with 43.4 ± 7.47 neonates for the *Chaoborus* treatment and 45.8 ± 11.0 neonates for the control (Table 1).

The mean clutch size for individuals grown in the *Lepomis* treatment (10.7 ± 0.47) was significantly greater (ANOVA, $P < 0.001$) than the mean clutch size of individuals grown in the control treatment (6.8 ± 0.98). In addition, individuals grown in the *Chaoborus* treatment (9.6 ± 0.93) produced significantly larger clutches than individuals grown in the control treatment (Table 1).

Predator treatment had a significant effect on ephippia production (Fisherex, $P = 0.0052$). Forty-seven per cent of the individuals in the *Lepomis* treatment produced ephippia compared with 13% of the individuals in the controls; no ephippia were ever produced in the *Chaoborus* treatment. Within the *Lepomis* treatment, ephippia were first produced on day 9 of the experiment. In contrast, the two individuals from the control treatment that produced ephippia did so on day 21 (Fig. 3). In addition, all of the individuals that produce ephippia in both the control and *Lepomis* treatment also produced parthenogenetic clutches of neonates.

Discussion

Daphnia lumholtzi was first reported in the United States in the early 1990s (Sorenson & Sterner, 1992; Havel & Hebert, 1993) and therefore this invader has had only a short evolutionary association with the invertebrate and vertebrate predator species used in this study. However, our results suggest that *D. lumholtzi* is able to respond, and discriminate between, kairomones released by different size-selective predators.

Predator-induced spine induction

Direct exposure to predator kairomones during post-embryonic development did not stimulate the production of the extravagant spines that are characteristic of natural *D. lumholtzi* populations. In contrast to our results, Tollrian (1994) reported that when individuals from a clone of *D. lumholtzi* from Fairfield Reservoir, Texas, were exposed to filtered water that previously held fish (*Leucaspius delineatus*), they developed significantly longer HS and TS than did control organisms, although not as long as those found in natural populations. Tollrian's (1994) results and the lack of a postembryonic response observed in our study, suggest that populations of *D. lumholtzi* within the United States exhibit clonal variability in their capacity to form long spines in response to direct exposure to predator kairomones.

We did find however, that pre-embryonic kairomone exposure had a significant effect on *D. lumholtzi* spine lengths. For example, individuals exposed to water conditioned by *Lepomis* kairomones produced neonates with significantly longer spines than the spines of neonates produced from the control and *Chaoborus* individuals (Fig. 2). Similarly, Yurista (2000) found that exposure to elevated temperatures had a greater maternal effect on spine induction in *D. lumholtzi* than on juveniles or adults. It should be noted however, that we continued to culture our neonates in their respective predator-conditioned media, and their spine lengths did not continue to increase with extended postembryonic exposure. As a result, the induced spines of our experimental neonates were not as long as those found in nature. These results suggest that several generations of pre-embryonic kairomone exposure may be necessary to induce the characteristically long spines in *D. lumholtzi*, or that additional environmental cues or combinations of cues, may be required for the maintenance and development of long spines (Yurista, 2000).

In addition, the spines induced in this study were not as long as those used in previous feeding-rate experiments (Swaffar & O'Brien, 1996). For example,

the average HS and TS lengths of individuals used in Swaffar & O'Brien (1996) were 0.51 and 1.46 mm, respectively. In contrast, the neonate HS and TS lengths induced by *Lepomis* kairomones were 0.25 and 0.51 mm, respectively (Fig. 2). Therefore, it is difficult to determine if these spines would directly affect predator-feeding rates, and additional experiments are needed to determine if the spines induced in neonates in this study are long enough to create handling difficulties for planktivorous fish.

Predator-induced morphological shifts

Exposure to predator kairomones resulted in morphological changes, independent of spine formation that may increase *D. lumholtzi*'s resistance to predation. For example, prior to first reproduction on day 3 only, individuals grown in the *Lepomis* treatment had smaller average CB lengths than individuals grown in the control (Fig. 4). Predator reaction distance is highly correlated with zooplankton core body size; therefore planktivorous fish are able to locate large zooplankton better (Conifer & Blades, 1975; O'Brien, 1987). A smaller CB length prior to first reproduction, which has been previously reported in *Daphnia* exposed to fish kairomones (Doksaeter & Vijverberg, 2001), thus increases the likelihood of successfully releasing the first brood into the water column before it attains a size vulnerable to detection by fish (Sakwinska, 2002).

Direct exposure to *Chaoborus* kairomones also had a significant effect on the morphology of *D. lumholtzi*. Individuals exposed to *Chaoborus* conditioned water had significantly smaller CB lengths than did control organisms (Fig. 4). These results appear to contradict current zooplankton life history theory, which suggests that in the face of invertebrate predation pressure, zooplankton should reach a larger body size at a faster rate (Dodson, 1974; Lynch, 1980; Black & Dodson, 1990). However, it is not uncommon for medium- to large-bodied species such as *D. lumholtzi* to attain a 'predation-safe' body size, at which handling efficiency by invertebrate predators decreases (Havel & Dodson, 1987; Black & Dodson, 1990). While we have not conducted feeding experiments, Swaffar & O'Brien (1996) noted that individuals >2 mm created handling difficulties for *Chaoborus* larvae. In our study, *D. lumholtzi* reared in *Chaoborus*-conditioned water reached this potentially predation-safe TB length by day 3 (Fig. 2). This may therefore allow these individuals to divert energy elsewhere, such as reproduction, than to further increase resistance to predation.

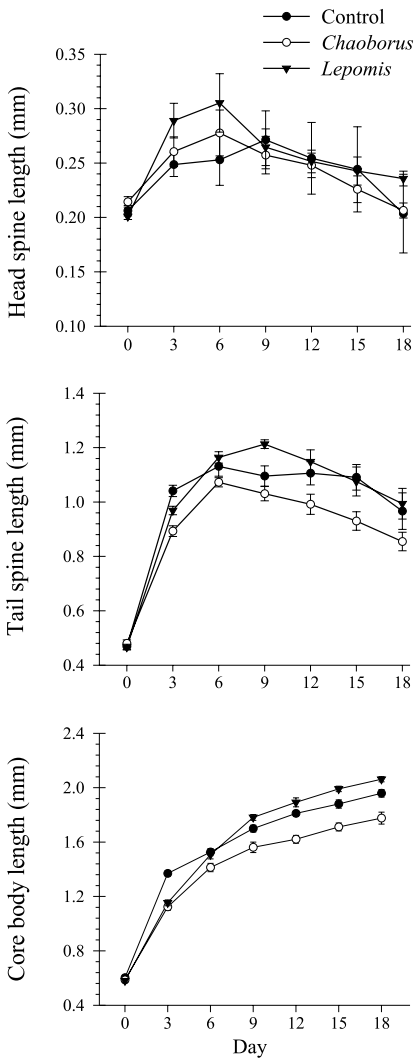

Fig. 4 Spine and body length measurements of *D. lumholtzi* grown in control, *Chaoborus*- and *Lepomis*-conditioned water, based on least square means obtained from RM-ANOVA. Error bars represent SEM; note that there is a difference in scale on the *y*-axes between graphs.

Predator-induced life history responses

Predator-induced shifts in the life history characteristics and resource allocation patterns of *D. lumholtzi* occurred independent of spine formation in this study. For example, all of the reproductive measures used in this study were consistently greatest for

D. lumholtzi grown in *Lepomis* kairomones relative to control and *Chaoborus* individuals (Table 1). Increased reproductive output of individuals exposed to fish kairomones in the absence of actual predation has been reported elsewhere and is consistent with current life history theory (O'Brien *et al*., 1980). For example, the theory predicts that under vertebrate predation where adult mortality is high, a larger number of offspring should be produced (Zaret, 1980; Taylor & Gabriel, 1992).

With respect to individuals grown in the *Chaoborus*-conditioned water, the age at first reproduction was significantly delayed compared with control individuals (Table 1). This response is common for *Daphnia* exposed to *Chaoborus* kairomones (Havel & Dodson, 1987; Black & Dodson, 1990; Black, 1993), and often results in a depressed population growth rate. As a result, delayed reproduction has been considered a cost of possessing morphological defences (Havel & Dodson, 1987; Black & Dodson, 1990). For example, Black (1993) found that *D. pulex* exposed to *Chaoborus* kairomones experienced a delay in the onset of first reproduction; however, these negative effects were dampened by an increase in the mean clutch size of exposed individuals. Similarly, in our study the mean clutch size of organisms grown in the *Chaoborus*-conditioned water was larger than the mean clutch size of control organisms (Table 1). As a result, the longer development time observed for individuals grown in the *Chaoborus* treatment was balanced by larger clutches, and there was no significant reduction in the intrinsic rate of increase (Table 1).

Predator-induced ephippia production

Exposure to *Lepomis* kairomones resulted in significantly more *D. lumholtzi* producing resting eggs, or ephippia. Recent studies have shown that the large-bodied *D. magna* also produces ephippia in response to fish kairomones (Slusarczyk, 2001; Pijanowska & Stolpe, 1996), and predator avoidance has previously been suggested as the ultimate cause of diapause in daphnids (Hairston, 1987). Under, stress daphnids produce ephippia that can remain viable for long periods of time and that can accumulate as a 'seed bank' in the lake sediment at high densities (see Hairston, 1996). When conditions become favourable for growth, ephippia hatch from the sediment and re-establish *Daphnia* populations. Moreover, the production of a resting stage provides both a means of dispersal and a temporal refuge that increases the likelihood of establishment (Hairston *et al*., 1999).

The exotic cladoceran *D. lumholtzi* exhibits a high degree of phenotypic plasticity in response to predaceous species that do not occur within its native range. Direct exposure to predator kairomones did not induce the development of characteristically long spines in *D. lumholtzi* in this study. However, our results suggest that there was a maternal effect of *Lepomis* kairomone exposure on spine development in the neonates produced by these individuals. Additionally, we observed several predator-induced shifts in the morphology and life history characteristics of *D. lumholtzi* that may further increase its resistance to predation. Future research investigating how these observed morphological and life history shifts affect both invertebrate and vertebrate predation rates is needed in order to determine if *D. lumholtzi*'s ability to respond to immediate predation pressures is an important factor reducing predation and ultimately contributing to the successful colonisation of new habitats.

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