Aquat Ecol (2006) 40:361–372
DOI 10.1007/s10452-006-9035-5

ORIGINAL PAPER

# Temperature and kairomone induced life history plasticity in coexisting *Daphnia*

**Randall J. Bernot · Walter K. Dodds · Michael C. Quist · Christopher S. Guy**

Received: 19 April 2005 / Accepted: 22 February 2006 / Published online: 27 April 2006


**Abstract** We investigated the life history alterations of coexisting *Daphnia* species responding to environmental temperature and predator cues. In a laboratory experiment, we measured *Daphnia* life history plasticity under different predation risk and temperature treatments that simulate changing environmental conditions. *Daphnia pulicaria* abundance and size at first reproduction (SFR) declined, while ephippia (resting egg) formation increased at high temperatures. *Daphnia mendotae* abundance and clutch size increased with predation risk at high temperatures, but produced few ephippia. Thus, each species exhibited phenotypic plasticity, but responded in sharply different ways to the same environmental cues. In Glen Elder reservoir, Kansas USA, *D. pulicaria* dominance shifted to *D. mendotae* dominance as temperature and predation risk increased from March to June in both 1999 and 2000. Field estimates of life history shifts mirrored the laboratory experiment results, suggesting that similar phenotypic responses to seasonal cues contribute to seasonal *Daphnia* population trends. These results illustrate species-specific differences in life history plasticity among coexisting zooplankton taxa.

**Keywords** *Daphnia pulicaria* · *Daphnia mendotae* · Life history · Phenotypic plasticity · Ephippia

R. J. Bernot · W. K. Dodds · M. C. Quist · C. S. Guy
Division of Biology, Kansas State University, Manhattan, KS 66506, USA

R. J. Bernot (✉)
Department of Biological Sciences, Murray State University, 334 Blackburn Science Building, Murray, KY 42071, USA
e-mail: rbernot@nd.edu
Fax: +1-270-762-2788

M. C. Quist
Natural Resource Ecology and Management, Iowa State University, 339 Science II, Ames, IA 50011-3221, USA

C. S. Guy
U.S. Geological Survey—Biological Resources Division, Montana Cooperative Fishery Research Unit, Department of Ecology, Montana State University, Bozeman, MT 59717-3460, USA

## Introduction

The ability of a given genotype to respond to distinct environmental conditions, termed phenotypic plasticity, has been studied extensively by evolutionary biologists (Pigliucci 2001; DeWitt and Scheiner 2004). Phenotypically plastic traits have been documented in practically all major groups of organisms at every trophic level (Tollrian and Harvell 1999; Pigliucci 2001). Organisms may have plastic behaviors, morphologies, and life histories that reflect trade-offs in the costs and benefits associated with factors such as predation risk (Reznick et al. 1996), resource acquisition (Tessier et al. 2000), or other

environmental gradients (Pigliucci 2001). Reaction norms describe plasticity by illustrating the function that relates trait values over a range of environments (Stearns 1992; Pigliucci 2001).

Most plasticity studies focus on single species population-level causes and consequences (Pigliucci 2001; Dewitt and Scheiner 2004). Recently, links between individual-scale trait plasticity and community dynamics suggest that plastic trait shifts have far-reaching food web and ecosystem impacts (Bernot and Turner 2001; Werner and Peacor 2003). Differential plastic responses of co-occurring species to the environment are likely, but largely unstudied (Relyea 2001).

Life history theory predicts that energy allocation within an individual determines growth, survival, and reproduction (Stearns 1992). Plastic life history shifts occur as optimal resource partitioning to either maternal growth (later reproduction, larger size at first reproduction, SFR) or earlier reproduction at smaller sizes with more eggs (Taylor and Gabriel 1992). Organisms trade-off the size and number of eggs they produce and the timing of reproduction by allocating resources to somatic tissue, growth or defenses (Stearns 1992). Alterations in life history traits may ultimately be manifested as increases in population growth through higher survival or higher fecundity, or may result in decreasing population size through resting egg formation (Stibor and Lampert 2000; Bernot et al. 2004a).

Here, we investigated the differential life history responses of two coexisting *Daphnia* species to an environmental gradient. In a laboratory experiment, we measured life history reaction norms of *Daphnia pulicaria* and *D. mendotae* at three levels of water temperature and with or without predation risk, representing the natural change of conditions in a freshwater reservoir. Patterns of abundance and life history trait values of field *Daphnia* populations were then related to laboratory patterns of phenotypic plasticity.

## Methods

### Study system

We studied *Daphnia* from Glen Elder Reservoir, a 5093 ha reservoir in Mitchell County, Kansas, USA. Resource use of *Daphnia pulicaria* and *D. mendotae* overlaps and these species compete for algae in this and other lakes (Leibold 1991; Hu and Tessier 1995; Cáceres 1998a; Bernot et al. 2004b). *Daphnia pulicaria* are larger (1.5–3.0 mm), have more pigments (Hu and Tessier 1995), and reproduce better at lower water temperatures than *D. mendotae* (1.0–2.0 mm). Single-clone batch cultures were established from individuals collected in the spring of 1999. Glen Elder Reservoir is relatively shallow (mean depth= 7 m), and was not stratified in either 1999 or 2000. Lack of a hypolimnetic refuge and turbulence associated with high wind speeds (often sustained >5 m $s^{-1}$) and long fetch (up to 7 km) constrain the vertical movement of these *Daphnia* species. Neither species showed large-scale diel vertical migration or distinct depth distribution patterns (Bernot et al. 2004b).

### Laboratory experiment

We tested whether temperature and predation risk cues led to differential life history responses of *Daphnia pulicaria* and *D. mendotae*. Predation risk (using bluegill sunfish kairomones) and temperature were manipulated, while maintaining constant resources to determine whether SFR, clutch size, ephippia production, and density of these two species depend on environmental context. Single clones of both *D. pulicaria* and *D. mendotae* established from parthenogenetic females taken from Glen Elder Reservoir were used. Experiments were conducted as batch cultures in 20 l glass containers in environmental chambers with a 12 h light: 12 h dark cycle in a split-plot design. Six containers were used in each of six different temperature trials. Each trial consisted of applying one of the predator treatments (with fish kairomone, without fish kairomone) to each of the six containers (three replicates per predator treatment) at one of three temperatures (15°C, 20°C, 25°C) over a 21-day period. Since only one environmental chamber was used, we repeated this procedure six times (two replicates per temperature treatment). Thus, 36 total experimental containers with 20 l of water were used (six containers in each of six temperature trials), resulting in six replicates of each treatment combination (i.e., the kairomone—20°C treatment combination was replicated three times in each of two 20°C trials). Five females of each species were randomly

chosen from a group of synchronously hatched juveniles raised from a single grandmother and placed in each container within 1-day of birth.

Experimental media was prepared from aged lake water aerated for 24 h to remove potential predatory cues originating from the lake (Barata et al. 2001). For fish cue treatments, 100 ml of water taken from 30 l aquaria housing 2 juvenile bluegills (i.e., 0.067 fish $l^{-1}$) was added to 900 ml of aerated lake water and placed in the respective containers daily. Previous experiments indicated that bluegill kairomone induced life history trait shifts similar to larval fish in *D. pulicaria* and *D. mendotae* (Bernot 2003). For the no kairomone treatments, 1 l of aged lake water was added to each container daily.

Prior to treatment additions, both fish cue and no-fish cue media were passed through a 0.45 μm filter to remove pre-existing algal cells and detritus before algae (*Scenedesmus acutus*; from culture) were added to an approximate cell density of $8\times10^4$ cells $ml^{-1}$ (>1 mg C $l^{-1}$), well above limiting resource conditions (Gliwicz 1990). Every day, 1 l of water from each container was carefully pipetted out and replaced with the appropriate treatment water described above. Algae were added at the above density daily to compensate for sedimentation and differential filtering rates between treatments due to different population densities.

At the conclusion of each experimental trial, the contents of each container were filtered through 64 μm mesh, fixed in 4% sugar formalin and subsequently preserved in 70% ethanol. All *Daphnia* were counted, and species, number of eggs, and the presence of ephippia was noted. Clutch size is reported as mean eggs per female calculated by counting subitaneous eggs in all egg-bearing females and dividing by the total number of females in a container. SFR was estimated by determining the size class in which >50% of the maximum percentage of egg-bearing females was reached (Stibor and Lampert 1993). We also estimated ephippial production as the number of ephippial-producing females in each sample. While many ephippia were found, resting eggs from each species could not be definitively distinguished.

## Statistical analysis

Differences in abundance, ephippial females, clutch size, and SFR between treatments were analyzed with MANOVA because the response variables were not independent. When MANOVA differences were significant ($\alpha = 0.05$), univariate analysis of variance for a split-plot design was used to detect differences in the dependent variables. Because one chamber was used for all temperature conditions, and experimental units differed for each effect (i.e., experimental unit for temperature effect was a chamber, but experimental unit for predation risk was a glass container), a split-plot design with chamber as the whole plot was used. Each temperature trial lasted 3 weeks, and each temperature was repeated once. Therefore, the whole plot factor, temperature, was in a completely randomized design with 3 factor levels and $n$=2. The within plot factor, predator kairomone, was completely randomized within each whole plot with 2 factor levels and $n$=3 for each trial ($n$=6 total for each treatment combination).

The trial×temperature interaction sums of squares was used to compute the proper $F$-test statistic for analyzing temperature as a whole-plot effect (Kuehl 2000). Multiple comparisons between factor levels were conducted with Tukeys multiple comparison. SYSTAT 8.0 was used in all analyses.

## Field sampling-Glen Elder Reservoir

We studied the plankton community of Glen Elder Reservoir in 1999 and 2000 with a particular focus on water temperature, the abundance of larval fish and the life history attributes of *D. pulicaria* and *D. mendotae*. We used larval fish density to indicate an increase in fish planktivory. We also assumed that chemical cues generated by feeding fish (kairomones) increased in concentration in the reservoir when larval fish emerged and consequently considered their effects on the life history traits of *Daphnia* (Mehner 2000). We monitored the *Daphnia* community and larval fish density weekly in Glen Elder Reservoir from 16-March to 8-June 1999 and from 21-March to 25-May 2000. Zooplankton and larval fish were sampled from 24 stations in 1999 and 20 stations in 2000. Full water-column zooplankton samples were collected with a Wisconsin plankton net (12 cm diameter, 65 μm mesh) and preserved in 70% ethanol. *Daphnia* were enumerated by counting all organisms in a 5 ml subsample on a counting wheel. Body length (top of eye to base of tail in mm) of 70 individuals of each species from each sample was

measured on a computer imaging system. Eggs from at least 50 egg-bearing females of each species were counted. If fewer than 50 egg-bearing females were found, then all were included in the analysis. Body length of each egg-bearing female was also measured. Twenty non egg-bearing females (i.e., juveniles, males, adult females without eggs) were measured along with 50 egg-bearing females, which were combined to obtain an overall mean body size for each species at each sampling period. SFR and ephippial production were estimated as described above. Clutch size was estimated by regressing egg number against female body length, and is reported here as a standardized clutch (not including females producing ephippia) size for females 1.3 mm in body length. Population growth rates ($r$; day$^{-1}$) were calculated from abundance ($N$) on two successive sampling dates ($t_1$ and $t_2$):

$$r = \frac{\ln(N_{t2}) - \ln(N_{t1})}{t_2 - t_1}. \quad (1)$$

We used the egg ratio method to calculate birth rates (day$^{-1}$) for each species (Paloheimo 1974):

$$b = \frac{\ln[(E/N) + 1]}{D} \quad (2)$$

based on the number of eggs per individual ($E/N$) and the temperature-dependent development time, $D$. Birth rates were calculated using both parthenogenic egg and ephippial producing (EP) females such that egg number for EP individuals was zero. Even though each ephippia contains two eggs, they necessarily undergo a diapause stage, and are not included as part of the immediate population. For *D. pulicaria*, development times were calculated using data from Gulbrandsen and Johnsen (1990) which provides development times for a related species, *D. pulex*. Development times of *D. mendotae* were calculated using data from Hall (1964). Death rates, $d$, in each population were estimated by taking the difference between birth ($b$) and population growth ($r$) rates.

Larval fish were sampled by pushing paired bongo nets (0.5 m diam., 500 μm mesh) from the bow of a boat at a depth of 0.5–1.5 m. Nets were deployed for approximately 5–10 min at a speed of 1.5 m s$^{-1}$. Sample volume was determined from flow meters fixed to the mouth of all nets. Ichthyoplankton samples were immediately preserved in 90% ethanol and transported back to the lab for processing. We define larval fish ''emergence'' as the sampling period in which >2 fish m$^{-3}$ were first collected. This definition is based on a spike of larval fish sampled in the spring of both sampling years. Two-way repeated measures analysis of variance with the effects species and time were used to determine if *Daphnia* abundance, mean body size, SFR, clutch size, ephippial production differed before and after larval fish emergence. Linear contrasts were used to compare samples taken before larval fish emergence and after larval fish emergence. Each sampling year (1999 and 2000) was analyzed separately.

## Results

### Laboratory experiment

*Daphnia pulicaria* life history traits and abundance depended on temperature, but not predation risk (Table 1). *Daphnia mendotae* life history traits depended on both temperature and predation risk (Table 1). *Daphnia pulicaria* abundance, SFR, clutch size, and ephippium production depended on temperature (Table 2). Abundance of *D. pulicaria* at 25°C was lower than at 15°C (Tukey's: $P<0.01$) or at 20°C (Tukey's: $P<0.01$). SFR at 25°C was significantly smaller than at 15°C (Tukey's: $P<0.01$) or at 20°C (Tukey's: $P=0.02$). *Daphnia pulicaria* produced fewer eggs at 25°C than at cooler temperatures (Tukey's: 15°C vs. 25°C, $P<0.01$ and 20°C vs. 25°C,

**Table 1** MANOVA results for the effects of predation risk (kairomones) and temperature on (A) *Daphnia pulicaria* and (B) *Daphnia mendotae* abundance and life history characteristics in a laboratory experiment. Note: Values are the Wilks' lambda $F$ statistic and the associated $P$ values

| Source of variation | df | $F$ | $P$ |
|---|---|---|---|
| *(A) Daphnia pulicaria* | | | |
| Predation risk | 4, 27 | 1.67 | 0.19 |
| Temperature | 8, 54 | 38.17 | <0.01 |
| Predation risk×temperature | 8, 54 | 2.97 | <0.01 |
| *(B) Daphnia mendotae* | | | |
| Predation risk | 4, 27 | 16.42 | <0.01 |
| Temperature | 8, 54 | 22.06 | <0.01 |
| Predation risk×temperature | 8, 54 | 7.46 | <0.01 |

**Table 2** Results of univariate split-plot ANOVA on the effects of predation risk (kairomones) and temperature on (A) *Daphnia* abundance, (B) SFR, (C) eggs per female, and (D) ephippial production in a laboratory experiment

| | Source of variation | df | *Daphnia pulicaria* | | *Daphnia mendotae* | |
|---|---|---|---|---|---|---|
| | | | *F* | *P* | *F* | *P* |
| *(A) Daphnia abundance* | | | | | | |
| Whole-plot | Temperature | 2 | 73.346 | <0.001 | 26.212 | 0.001 |
| | Trial | 1 | | | | |
| | Error (whole plot) | 2 | | | | |
| Sub-plot | Predation risk | 1 | 1.448 | 0.268 | 4.019 | 0.085 |
| | Predation risk×temperature | 2 | 2.195 | 0.182 | 4.421 | 0.074 |
| | Error | 9 | | | | |
| *(B) SFR* | | | | | | |
| Whole-plot | Temperature | 2 | 28.367 | 0.003 | 3.876 | 0.083 |
| | Trial | 1 | | | | |
| | Error (whole plot) | 2 | | | | |
| Sub-plot | Predation Risk | 1 | 0.001 | 0.978 | 11.813 | 0.014 |
| | Predation risk×temperature | 2 | 2.632 | 0.132 | 7.996 | 0.020 |
| | Error | 9 | | | | |
| *(C) Eggs per female* | | | | | | |
| Whole-plot | Temperature | 2 | 22.906 | 0.015 | 657.331 | <0.001 |
| | Trial | 1 | | | | |
| | Error (whole plot) | 2 | | | | |
| Sub-plot | Predation risk | 1 | 0.001 | 0.972 | 5.365 | 0.046 |
| | Predation risk×temperature | 2 | 0.001 | 0.987 | 11.528 | 0.003 |
| | Error | 9 | | | | |
| *(D) Ephippial production* | | | | | | |
| Whole-plot | Temperature | 2 | 762.584 | <0.001 | 1.363 | 0.337 |
| | Trial | 1 | | | | |
| | Error (whole plot) | 2 | | | | |
| Sub-plot | Predation risk | 1 | 0.023 | 0.883 | 0.001 | 0.999 |
| | Predation risk×temperature | 2 | 0.023 | 0.883 | 0.144 | 0.715 |
| | Error | | | | | |

$P<0.01$). More females with ephippia were present at higher temperatures than at 15°C (Tukey's: 15°C vs. 20°C, $P<0.01$ and 15°C vs. 25°C, $P<0.01$). Kairomones had no significant effect on *D. pulicaria* abundance, SFR, clutch size, and ephippium production, however (Table 1). Since sexually produced ephippia result in fewer offspring per generation (e.g., 2) than parthenogenetically produced juveniles (e.g., 10–20), a shift in the reproductive mode of *D. pulicaria* females would account for the lower observed abundances.

In contrast, only abundance of *D. mendotae* depended solely on temperature (Table 1A). Abundance of *D. mendotae* at 25°C was higher than at 15°C (Tukey's $P<0.01$) and at 20°C (Tukey's $P<0.01$). Kairomone effects on *D. mendotae* SFR depended on temperature (Table 1B, significant kairomone× temperature interaction). Females reproduced at a smaller size in the presence of kairomones (Tukey's: kairomone versus no kairomone, $P<0.01$), but only at 20°C and 25°C (Fig. 1). Kairomone effects on *D. mendotae* clutch size also depended on temperature (Table 1C). Clutch size was greatest at 25°C (Tukey's: 15°C vs. 25°C, $P<0.01$ and 20°C vs. 25°C, $P<0.01$). *Daphnia mendotae* produced few ephippia even at high temperatures, while *D. pulicaria* started producing ephippia between 15°C and 20°C.

## Field abundance and life history

In both years, the abundance of both species changed dramatically after larval fish emerged and water temperatures exceeded 17°C (Fig. 2; Table 3). The two *Daphnia* species did not significantly differ in body size prior to and at the time of larval fish emergence (Table 1B; linear contrast: $P=0.25$). The zooplankton community changed from a few species dominated by *D. pulicaria* early in the spring to a more diverse community dominated by *D. mendotae* in May and June of both study years and is reported elsewhere (Bernot et al. 2004b).

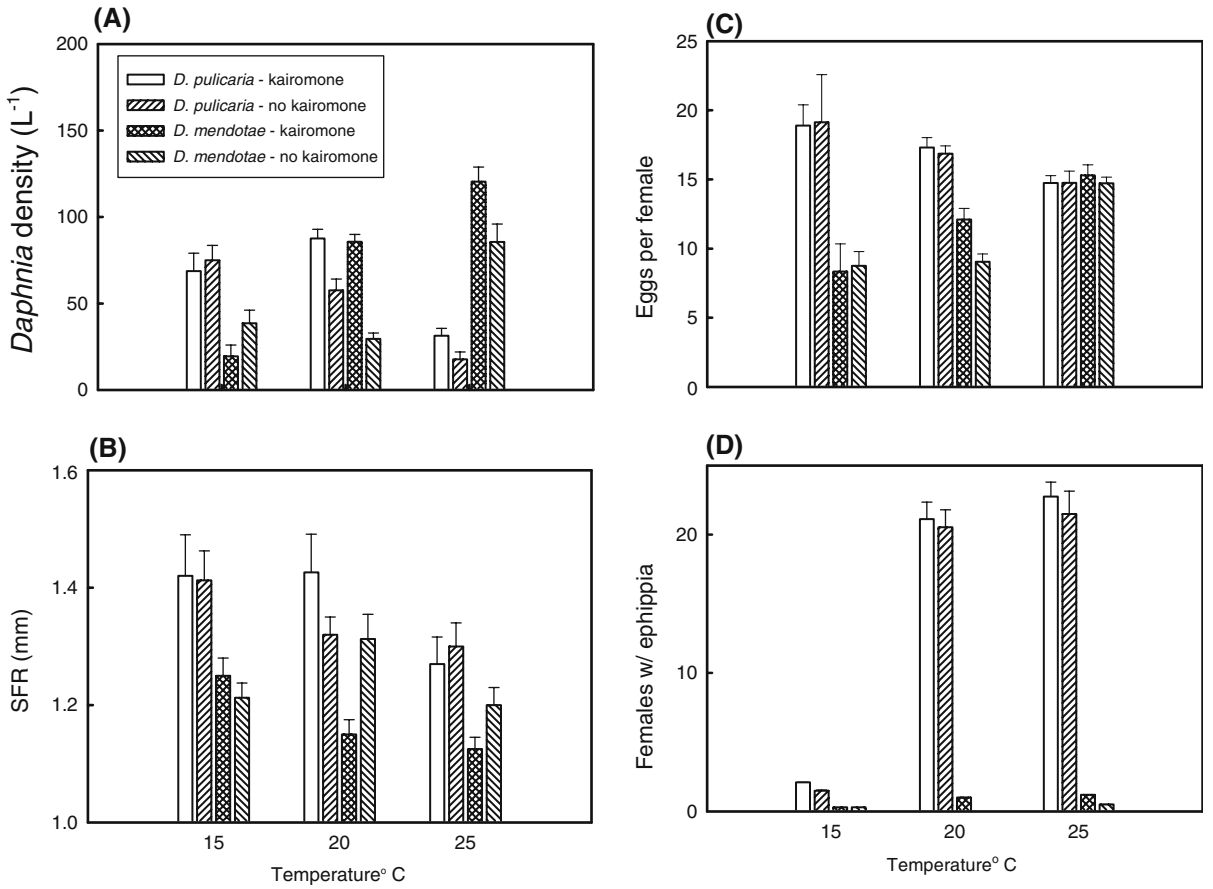


**Fig. 1** Effects of temperature and predation risk on *Daphnia* life history and abundance. *Daphnia* **A** abundance, **B** SFR, **C** eggs per female, and **D** number of females with ephippia in simulated *Daphnia* communities under combinations of temperature and predation risk (presence or absence of fish kairomones) treatments. Bars represent mean value±SE ($n$=6)

The life history attributes of both *D. pulicaria* and *D. mendotae* differed after this environmental change of rising temperature and increasing predation risk (Table 3; Fig. 3). *Daphnia mendotae* reproduced at a smaller size (SFR) and produced more eggs after larval fish emerged (Fig. 3A, B; linear contrast: $P$<0.01). *Daphnia pulicaria* SFR and clutch size did not differ after larval fish emergence, but the production of ephippial resting eggs increased (Fig. 3E, F; linear contrast: $P$<0.01). Birth and death rates of both *Daphnia* species were similar before larval fish emerged, but were significantly different after larval fish emergence (Fig. 4; linear contrasts: $P$<0.01). Birth rates of *D. pulicaria* decreased in May of both years, while *D. mendotae* birth rates increased steadily through the sampling periods (Fig. 4).

## Discussion

*Daphnia pulicaria* and *D. mendotae* exhibited differential responses to the environment across a temperature gradient. At low temperatures, *D. pulicaria* clutch size, SFR, and abundance were greatest, but these trait values declined at high temperature. Resting egg production in *D. pulicaria*, however, was induced by high temperature. The life history reaction norms of *D. mendotae* contrasted with those of *D. pulicaria*. *Daphnia mendotae* clutch size, SFR, and abundance were greatest at high water temperatures, while resting egg production did not differ across environmental conditions. Fish kairomone also affected *D. mendotae* SFR, inducing smaller SFR at high water temperatures. Phenotypic alterations were induced solely by temperature in *D. pulicaria* and

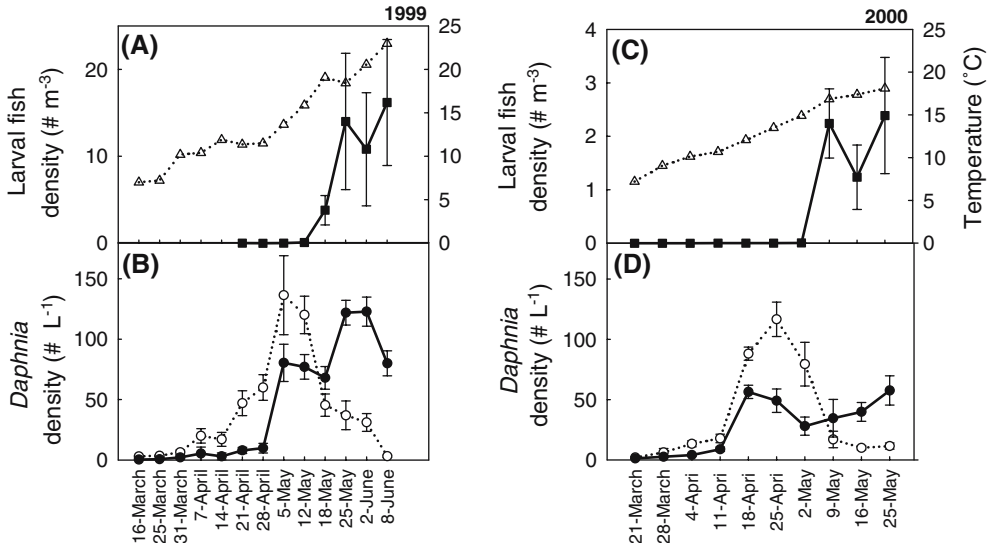


**Fig. 2** Patterns of larval fish and *Daphnia* abundance in Glen Elder Reservoir, Kansas, USA. **A** Larval fish density (closed circles, solid line) and water temperature (open triangles, dotted line) in 1999; **B** *Daphnia pulicaria* (open circles, dotted line) and *D. mendotae* (closed circles, solid line) abundance in 1999; **C** larval fish density and water temperature in 2000; **D** *D. pulicaria* and *D. mendotae* abundance in 2000. Symbols represent mean±SE ($n$=24 sampling stations in 1999 and $n$=20 sampling stations in 2000)

were induced by both water temperature and fish cues in *D. mendotae*.

Across 2 years in Glen Elder Reservoir, *D. pulicaria* dominated in early spring, gradually declined in abundance, and then disappeared from the community in the summer (Bernot et al. 2004b). The dominant zooplankton species then became *D. mendotae* in late spring and throughout the summer (Fig. 2; Bernot et al. 2004b). The species dominance shift occurred along a temporal gradient represented by the laboratory experiment treatments: low water temperature and low predation risk in early spring, then warm temperatures and high predation risk (represented by greater larval fish densities) later in the season. Estimates of life history trait values (Fig. 3) from the natural populations mirrored the reaction norms observed in the laboratory experiment (Fig. 1), suggesting that phenotypically plastic trait shifts may have contributed to the observed *Daphnia* population patterns.

Warmer water temperature leads not only to larval fish hatching and growth, but to greater foraging activity of adult fishes. Thus, the direct predatory impact of fish on *Daphnia* populations is likely to increase in the spring, particularly with the abrupt increase in planktivores caused by hatching of larval fish. Size-selective foraging by fish on larger individuals and larger species can result in shifts in size distribution (Threlkeld 1979), species dominance (Mittelbach 1981), and spatial distribution (Leibold and Tessier 1991). Of the two species in this study, *D. pulicaria* has been found by others to be larger, more conspicuous, and more susceptible to visual foragers such as fish (Leibold and Tessier 1991). While SFR of *D. mendotae* was always smaller than that of *D. pulicaria*, overall mean body size of both species did not significantly differ on any sampling date in either year despite a large sample size (Table 3). Estimations of conspicuousness between the *Daphnia* species in Glen Elder Reservoir were not made; however it is likely that *D. pulicaria* carrying ephippia are highly conspicuous due to melanin pigmentation (Gerrish and Cáceres 2003). Analysis of stomach contents indicated that larval white bass (*Morone chrysops*) in Glen Elder preferentially consumed *Bosmina* and copepods (Quist et al. 2002). Walleye (*Stizostedion vitreum*) larvae stomach contents in enclosure experiments contained more *D. pulicaria* relative to its availability in the environment, suggesting selective predation (Bernot et al. 2004a). Walleye, however, constituted less than 1% of the larval fish community that was dominated by gizzard shad and white bass (*Dorosoma cepedianum*; Quist et al. 2002). Thus, it is likely that larval fish and

adult fish (not considered in this study) preferentially remove *D. pulicaria* allowing *D. mendotae* populations to increase.

The relative roles of direct fish predation and differential life history trait shifts towards seasonal succession have not been studied directly. Conventional hypotheses rely on direct predation and competition (Sommer 1989), yet these direct effects are in and of themselves strong selection pressures (Reznick et al. 1996). Thus, we might expect prey species to possess adaptations that allow survival during periods of unfavorable environmental conditions (e.g., high predation pressures). Sexual reproduction and ephippial production in *D. pulicaria* appear to be such an adaptation. Our study illustrates that sexual reproduction and ephippial production in *D. pulicaria* is induced by high water temperatures, making it a phenotypically plastic trait. Water temperature may be a reliable cue indicating an increase in future predation pressure. By forming ephippia before the emergence of larval fish, *D. pulicaria* produce eggs that can survive fish predation, potentially contributing to long term persistence in the lake (Cáceres 1997).

**Table 3** Results of repeated-measures ANOVA on the effects of species and time on *Daphnia* in Glen Elder Reservoir, Kansas USA (A) abundance, (B) mean body length, (C) size at first reproduction, and (D) clutch size

| Source of variation | 1999 | | | 2000 | | |
|---|---|---|---|---|---|---|
| | df | *F* | *P* | df | *F* | *P* |
| *(A) Daphnia abundance* | | | | | | |
| Species | 1 | 10.83 | <0.01 | 1 | 8.07 | <0.01 |
| Error | 46 | | | 38 | | |
| Time | 12 | 23.98 | <0.01 | 9 | 40.64 | <0.01 |
| Species×time | 12 | 12.54 | <0.01 | 9 | 48.33 | <0.01 |
| Error | 552 | | | 342 | | |
| *(B) Mean body length* | | | | | | |
| Species | 1 | 1.37 | 0.148 | 1 | 2.08 | 0.21 |
| Error | 46 | | | 38 | | |
| Time | 12 | 0.70 | 0.66 | 9 | 0.95 | 0.47 |
| Species×time | 12 | 1.04 | 0.11 | 9 | 1.12 | 0.11 |
| Error | 552 | | | 342 | | |
| *(C) SFR* | | | | | | |
| Species | 1 | 33.97 | <0.01 | 1 | 51.12 | <0.01 |
| Error | 46 | | | 38 | | |
| Time | 12 | 1.56 | 0.08 | 9 | 1.33 | 0.05 |
| Species×time | 12 | 2.98 | 0.02 | 9 | 2.09 | 0.02 |
| Error | 552 | | | 342 | | |
| *(D) Clutch size* | | | | | | |
| Species | 1 | 98.43 | <0.01 | 1 | 71.25 | 0.01 |
| Error | 46 | | | 38 | | |
| Time | 12 | 0.932 | 0.12 | 9 | 1.28 | 0.08 |
| Species×time | 12 | 3.15 | <0.01 | 9 | 3.48 | <0.01 |
| Error | 552 | | | 342 | | |
| *(E) Ephippial production* | | | | | | |
| Time | 12 | 65.05 | <0.01 | 9 | 32.75 | <0.01 |
| Error | 276 | | | 171 | | |

Results of repeated-measures ANOVA on the effects of time on *Daphnia pulicaria* (E) ephippial production. Note that no *D. mendotae* ephippial females were collected, and ephippial production was not analyzed for this species

Fish and fish kairomones are likely to be present in lakes and reservoirs throughout the year. However, since fish kairomone concentration has yet to be successfully measured in the field (Stibor and Lampert 2000), we can only assume that kairomone concentration increases above background levels in the spring when large numbers of larval fish become planktivorous and older fish begin to increase their feeding activity. We contend that fish-produced kairomones increase when larval fish emerge because even though the total fish biomass is unlikely to change, the density of individual fish actively feeding on *Daphnia* should rise sharply.

Despite similar patterns of life history and abundance in both the laboratory and field data, we can not attribute *Daphnia* seasonal dominance shifts to phenotypically plastic trait shifts. Our laboratory experiment measured the reaction norms of a single clone. Yet, multiple clones of each species likely occur in most lentic systems, potentially leading to clonal selection (Spitze 1991). Thus, an interclonal experimental factor must be included to link evolutionary processes to this planktonic community (Pfrender et al. 2000). Numerous studies document the adaptive nature of induced trait shifts in *Daphnia* and other organisms (Tollrian and Harvell 1999; Pigliucci 2001). Studies that explicitly link phenotypic plasticity, clonal diversity, and community and ecosystem processes will be a useful step in assessing the role of evolutionary processes in broader ecological dynamics (Chase 1999).

Similar systems with the same *Daphnia* species have been studied extensively elsewhere (Leibold and Tessier 1998; Cáceres 1997, 1998a, b). *Daphnia pulicaria* and *D. mendotae* compete for algal resources in lakes throughout North America (Hu and Tessier 1995; Cáceres 1998b). Leibold and Tessier (1998) found *D. pulicaria* and *D. galeata mendotae*

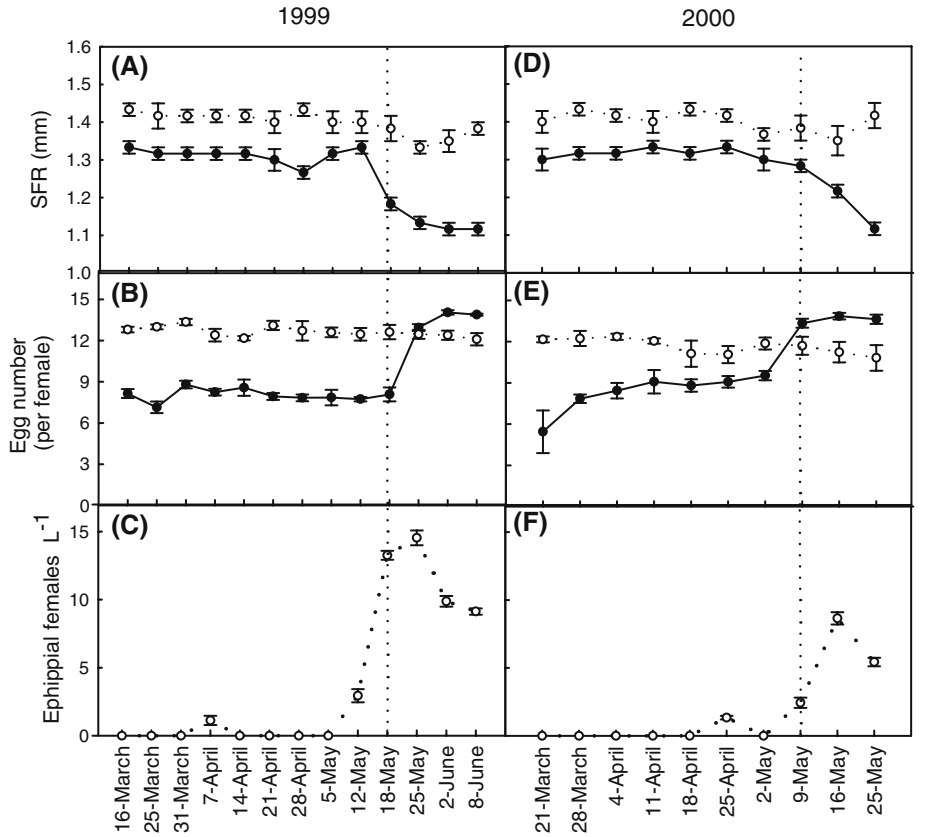


**Fig. 3** Life history traits of *Daphnia pulicaria* (open symbols and dotted lines) and *Daphnia mendotae* (closed circles and solid lines) in 1999 **A**, **B**, **C** and 2000 **D**, **E**, **F** from Glen Elder Reservoir. **A** and **D** display SFR. **B** and **E** display *Daphnia* mean clutch sizes per female. **C** and **F** display ephippial females. Symbols represent the mean value±SE ($n$=3). Vertical lines indicate larval fish emergence (i.e. when >2 larval fish $m^{-3}$ were sampled). Note that no ephippial females of *Daphnia mendotae* were sampled in either year

to coexist by occupying different depths in the water column along a gradient of predation risk. *Daphnia pulicaria* occupied deeper, cooler water in stratified lakes, while *D. galeata mendotae* underwent diel vertical migration. Thus, species coexistence was promoted by behavioral differences between species that reflect a trade-off between growth and predation susceptibility. The lack of vertical stratification in Glen Elder Reservoir, however, likely imposed a constraint on habitat segregation by depth (Bernot et al. 2004b). In fact, neither species exhibited large-scale vertical migrations, nor did they occupy different water column depths.

The induction of diapause via ephippia in *Daphnia* can be triggered by short photoperiod (Stross 1971), low food concentration (D'Abramo 1980), crowding (Carvalho and Hughes 1983). low temperature (Mortimer 1935), and chemical cues associated with fish predation (Ślusarczyk 1999; Alekseev and Lampert 2001). Diapause is a strategy against seasonally changing selective events and is usually initiated well before the environmental change. Furthermore, diapause may be induced by a predictable and cyclically varying cue such as temperature, which is associated with fish emergence and activity.

Environmentally induced life history adjustments are common in both plants (Grime et al. 1986; Pigliucci 2001) and animals (Tollrian and Harvell 1999). Examples from aquatic animals include zooplankton (Burks et al. 2000; Stibor and Lampert 2000, Lass and Spaak 2003), freshwater snails (Chase 1999), fish (Reznick et al. 1996), and mayflies (Peckarsky et al. 2002). In most cases, animals adjust their life histories in response to food and predation factors by reallocating resources to reproduction, somatic growth, or defense. Chemical cues from feeding predators are

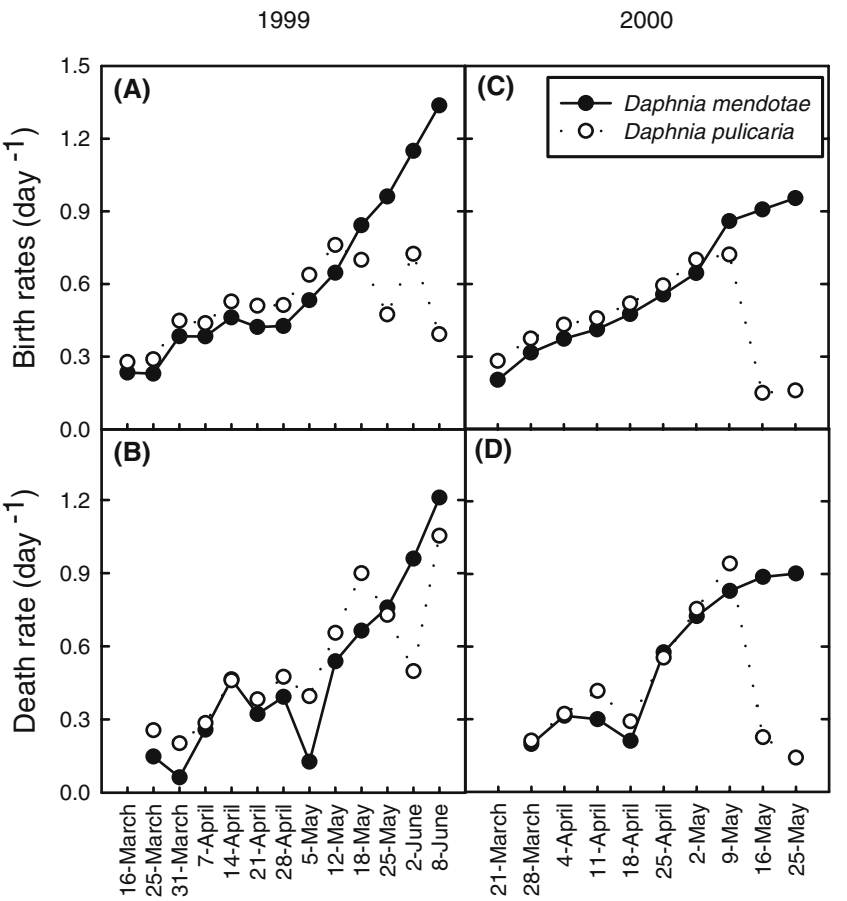


**Fig. 4** Birth rates **A**, **C** and death rates **B**, **D** of *Daphnia pulicaria* and *Daphnia mendotae* in 1999 and 2000 in Glen Elder Reservoir

often cited as reliable cues that induce life history shifts (Tollrian and Harvell 1999; Stibor and Lampert 2000). Temperature has rarely been considered to induce life history adjustments (but see Sakwinska 1998). Yet, seasonal temperature changes may provide the most reliable cue necessary for potentially adaptive phenotypic shifts. Our study illustrated phenotypically plastic life history shifts of *D. pulicaria* and *D. mendotae* due to warm water temperature and to a lesser extent fish cues in laboratory conditions. *Daphnia* populations in a reservoir exhibited qualitatively similar life history changes as laboratory populations. Our results illustrate species-specific differences in life history plasticity among coexisting zooplankton taxa and emphasize the role temperature plays in *Daphnia* life history.

**Acknowledgements** We thank M. Bernot, C. Oppert, S. Butler, J. Delp, J. Hart, K. Gido, N. Gerlanc, C. Smith, K. Kemp, J. Nechols, J. Trexler, and G. Lamberti. We also thank three anonymous reviewers for comments on previous versions of this manuscript and K. Austin and the staff at Glen Elder State Park for their assistance with this and other research on Glen Elder Reservoir. Funding was provided by the Kansas Department of Wildlife and Parks through Federal Aid in Sport Fish Restoration, Project F-45-R2 and Kansas State University.

## References

Alekseev V, Lampert W (2001) Maternal control of resting-egg production in *Daphnia*. Nature 414:899–901

Barata C, Baird DJ, Soares AMVM (2001) Phenotypic plasticity in *Daphnia magna* Straus: variable maturation instar as an adaptive response to predation pressure. Oecologia 129:220–227

Bernot RJ (2003) Ecological concsequences of *Daphnia* phenotypic plasticity in a Great Plains reservoir. PhD Dissertation, Kansas State University, Manhattan, Kansas USA, 127 pp

Bernot RJ, Turner AM (2001) Predator identity and trait-mediated indirect effects in a littoral food web. Oecologia 129:139–146

Bernot RJ, Dodds WK, Quist MC, Guy CS (2004a) Larval fish-induced phenotypic plasticity of coexisting *Daphnia*: an enclosure experiment. Freshw Biol 49:87–97

Bernot RJ, Dodds WK, Quist MC, Guy CS (2004b) Spatial and temporal variability of zooplankton in a Great Plains reservoir. Hydrobiologia 525: 101–112

Burks RL, Jeppesen E, Lodge DM (2000) Macrophyte and fish chemicals suppress *Daphnia* growth and alter life history traits. Oikos 88:139–147

Cáceres CE (1997) Temporal variation, dormancy, and coexistence: a field test of the storage effect. Proc Natl Acad Sci USA 94:9171–9175

Cáceres CE (1998a) Interspecific variation in the abundance, production and emergence of *Daphnia* diapausing eggs. Ecology 79:1699–1710

Cáceres CE (1998b) Seasonal dynamics and interspecific competition in Oneida Lake *Daphnia*. Oecologia 115: 233–244

Carvalho GR, Hughes RN (1983) The effect of food availability, female culture-density and photoperiod on ephippia production in *Daphnia magna* Straus (Crustacea: Cladocera). Freshw Biol 13:37–46

Chase JM (1999) To grow or to reproduce? The role of life history plasticity in food web dynamics. Am Nat 154:571–586

D'Abramo LR (1980) The stimulus for the asexual-sexual switch in *Moina macrocopa*. Limnol Oceanogr 25:422–429

DeWitt TJ, Scheiner SM (eds) (2004) Phenotypic plasticity: functional and conceptual approaches. Oxford University Press

Gerrish GA, Cáceres CE (2003) Genetic versus environmental influence on pigment variation in the ephippia of *Daphnia pulicaria*. Freshw Biol 48:1971–1982

Gliwicz ZM (1990) Food thresholds and body size in cladocerans. Nature 343:638–640

Grime JP, Crick JC, Rincon JE (1986) The ecological significance of plasticity. In: Jennings DH, Trewava AJ (eds) Plasticity in plants. Pindar Scarborough, North Yorkshire, pp 5–29

Gulbrandsen J, Johnsen GH (1990) Temperature-dependent development of parthenogenetic embryos in *Daphnia* pulex de Geer. J Plank Res 12:443–453

Hall DJ (1964) An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. Ecology 45:94–112

Hu SS, Tessier AJ (1995) Seasonal succession and the strength of intra- and interspecific competition in a *Daphnia* assemblage. Ecology 76:2278–2294

Kuehl RO (2000) Design of experiments: statistical principles of research design and analysis. Duxbury Press

Lass S, Spaak P (2003) Chemically induced anti-predator defences in plankton: a review. Hydrobiologia 491:221–239

Leibold MA (1991) Trophic interactions and habitat segregation between competing *Daphnia* species. Oecologia 86:510–520

Leibold MA, Tessier AJ (1991). Contrasting patterns of body size for coexisting *Daphnia* species that segregate by habitat. Oecologia 86:342–348

Leibold MA, Tessier AJ (1998) Experimental compromise and mechanistic approaches to the evolutionary ecology of interacting *Daphnia* species. In: Resetarits WJ Jr, Bernardo J (eds) Experimental ecology: issues and perspectives. Oxford University Press, pp 96–112

Mehner T (2000). Influences of spring warming on the predation rate of underyearling fish on *Daphnia* – a deterministic simulation approach. Freshw Biol 45:253–263

Mittelbach GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370–1386

Mortimer CH (1935) Untersuchungen über den generationsweschel der Cladoceran. Naturwissenschaften 23:473–480

Paloheimo JE (1974) Calculation of instantaneous birth rate. Limnol Oceanogr 19:692–694

Peckarsky BL, McIntosh AR, Taylor BW, Dahl J (2002) Predator chemicals induce changes in mayfly life history traits: a whole stream manipulation. Ecology 83:612–617

Pfrender ME, Spitze K, Lehmann N (2000) Multi-locus genetic evidence for rapid ecologically based speciation in *Daphnia*. Mol Ecol 9:1717–1735

Pigliucci M (2001) Phenotypic plasticity: beyond nature and nurture. Johns Hopkins University

Quist MC, Guy CS, Bernot RJ (2002) Ecology of larval white bass in a large Kansas reservoir. N Am J Fish Manage 22:637–642

Relyea RA (2001) Morphological and behavioral plasticity of larval anurans in response to different predators. Ecology 82:523–540

Reznick DN, Butler MJI, Rodd FH, Ross P (1996) Life history evolution in guppies (*Poecilia reticulata*). 6. Differential mortality as a mechanism for natural selection. Evolution 50:1651–1660

Sakwinska O (1998) Plasticity of *Daphnia magna* life history traits in response to temperature and information about a predator. Freshw Biol 39:681–687

Ślusarczyk M (1999) Predator-induced diapause in *Daphnia* magna may require two chemical cues. Oecologia 119:159–165

Sommer U (1989) Plankton ecology: succession in plankton communities. Springer-Verlag

Spitze K (1991) Chaoborus predation and life-history evolution in *Daphnia pulex*: temporal pattern of population diversity, fitness, and mean life history. Evolution 45:82–92

Stearns SC (1992) The evolution of life histories. Oxford University Press

Stibor H, Lampert W (1993) Estimating the size at maturity in field populations of *Daphnia* (Cladocera). Freshw Biol 30:433–438

Stibor H, Lampert WH (2000) Components of additive variance in life-history traits of *Daphnia hyalina*: seasonal differences in the response to predator signals. Oikos 88:129–138

Stross R (1971) Photoperiodism and diapause in *Daphnia*: a strategy for all seasons. Trans Am Micro Soc 90:110–112

Taylor BE, Gabriel W (1992) To grow or not to grow: optimal resource allocation for *Daphnia*. Am Nat 139: 248–266

Tessier AJ, Leibold MA, Tsao J (2000) A fundamental trade-off in resource exploitation by *Daphnia* and consequences to plankton communities. Ecology 81:826–841

Threlkeld ST (1979) The midsummer dynamics of two *Daphnia* species in Wintergreen Lake, Michigan. Ecology 60:165–179

Tollrian R, Harvell CD (eds) (1999) Ecology and evolution of inducible defenses. Princeton University Press

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100