



Life history comparisons of *Daphnia obtusa* from temporary ponds, cultured with a low-quality food

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Abstract

Temporary pond *Daphnia* flourish on relatively poor-quality food, suggesting adaptation to stringent temporary pond conditions. We conducted laboratory life history experiments on populations of *Daphnia obtusa* from a shaded woodland temporary pond (short hydroperiod, dystrophic) and an open farmland temporary pond (long hydroperiod, eutrophic), and compared a suite of physical/chemical conditions in the ponds to evaluate habitat conditions. We hypothesized that the shaded woodland pond population would be more fit in terms of life history variables for individuals (age and size at first reproduction, mean brood size, mean number of neonates) and populations (generation time, net reproductive rate R_0 , and intrinsic reproductive rate r) given a standard, low-quality food (trout chow and yeast). Life history traits of woodland pond animals were mixed, relative to farm pond animals, and consistent with bet-hedging for an unpredictable habitat. Values of life history traits rivaled or exceeded those of other studies using phytoplankton as food, and were influenced by the pond water used for our study. Life histories clearly differ among local and regional temporary pond *Daphnia obtusa* populations, and should be valuable for examining the relative influences of local selection and metapopulation dynamics on population structure.

Introduction

Life history traits result from the interplay between inheritance and selection on a population for a given environment. A substantial literature exists on *Daphnia* life history, but most of it regards animals from permanent waters and phytoplankton food quality (e.g., Gulati & Demott, 1997). Stearns (1976) reviewed life history traits of organisms living in various types of environments, including environments that fluctuate unpredictably (e.g., temporary ponds). Life history characteristics most beneficial in such habitats include: younger age and smaller size at first reproduction, high reproductive effort, small size of young, and high number of young per brood (Stearns, 1976). Selection in unpredictably-fluctuating environments should favor mixed life history strategies (e.g., producing some progeny early, and others later); a

strategy known as bet-hedging (Stearns, 1976, 1992; Phillipi & Seger, 1989).

Temporary ponds are natural, endorheic bodies of water which experience a recurrent dry phase of varying duration (Wiggins et al., 1980; Williams, 1987; Collinson et al., 1995). Physical and chemical conditions can change markedly in temporary ponds, and aquatic organisms must cope with these fluctuations as well as the transient habitat (Wiggins et al., 1980). Furthermore, temporary ponds exist in diverse locations (e.g., forests, prairie, etc.), so that it is likely that temporary ponds vary considerably in habitat quality for any given species. Therefore, aquatic organisms should experience strong selection within temporary ponds, and different suites of selective forces among temporary ponds.

Woodland temporary ponds are often dystrophic, due to high allochthonous input of organic matter

(leaf fall), which leads to high dissolved organic matter (DOM), low pH, and low dissolved oxygen. Nutrients are abundant in many woodland temporary ponds, due to enhanced microbial breakdown of organic material during drying/wetting cycles (Wiggins et al., 1980). However, phytoplankton in woodland temporary ponds can be limited by multiple factors, including: low pH (e.g., pH 5) and high humic substances content (Thomas, 1997); binding of soluble nutrients and phosphatase by DOM (Wiggins et al., 1980; Boavida & Wetzel, 1998); terrestrial detritus (Wehr et al., 1998); and shading from the tree canopy.

Therefore, *Daphnia* in woodland temporary ponds likely feed more on heterotrophic foods (i.e., seston (bacteria + detritus) and heterotrophic flagellates) than on autotrophic foods (i.e., phytoplankton). *Daphnia* can feed on all of the above (DeMott, 1982; Jones et al., 1999; Hessen & Andersen, 1990; Salonen et al., 1992), but seston can limit growth and reproduction relative to phytoplankton alone (Müller-Navarra & Lampert, 1996; Montel & Lair, 1997), and *Daphnia* prefer algae to bacteria (Urabe & Watanabe, 1991; Hart & Jarvis, 1993). In addition, *Daphnia* and other herbivores can be energetically-limited by low light conditions in shaded ponds, despite high nutrient availability (Urabe & Sterner, 1996). Based on these results, food quality should be one factor (among others) that limits success of *Daphnia* in woodland temporary ponds.

Despite potentially low food quality and other limitations, woodland temporary ponds and other humic waters often support dense populations of *Daphnia* and other filter-feeders (Kenk, 1949; Mahoney et al., 1990; Salonen et al., 1992). One explanation for this observation is that temporary pond populations have adapted to foods that would be considered low-quality for populations from permanent waters. If so, populations from different temporary ponds should differ in life history, and should differ from populations in permanent waters.

Considerable attention in aquatic ecology has been directed toward the effects of varying phytoplankton composition and nutrient content on *Daphnia* life history, especially in the contexts of delineating culture conditions (e.g., Keating, 1985) and trophic interactions in lakes (e.g., Matveev & Balsiero, 1990; Sterner et al., 1993). The mixture of trout chow and yeast (TCY) has been repeatedly considered a low-quality diet relative to algae: *Daphnia* cultured on this diet grow slower, produce fewer offspring, and survive less than *Daphnia* fed algae (Hall, 1964; Goulden et al.,

1982; Tessier et al., 1982; Dodson & Frey, 1991; Michels & DeMeester, 1998). We considered TCY to be a standardized food of documented low quality for *Daphnia*.

The purpose of this research was to compare *Daphnia obtusa* life history traits for 2 populations, given a standard, low-quality food. We expected that animals from a shaded woodland temporary pond would be better adapted to low-quality food than an open farmland temporary pond (with a longer hydroperiod) population, and that this difference would be exhibited in life history traits. According to Stearns (1976), the woodland pond population would be expected to exhibit a more mixed life history strategy than the farm pond population. In addition, we evaluated the effects of pond water on life history traits by culturing each population in water from each pond.

Methods

Study sites

The vernal woodland pond is located in Cass County, IL, 12 km east of Beardstown (Pond D4 in the Bluff Springs Sand Ponds). The site is dominated by silver maple (*Acer saccharinum*), river birch (*Betula nigra*) and elm (*Ulmus rubra*) trees. This area has a seasonally high water table and low surface runoff, which generates ponding, generally from March to June (Calsyn et al., 1989).

The open farm pond is located approximately 2.4 km southwest of the woodland pond site (10 km southeast of Beardstown). In contrast to the woodland pond, the farm pond is unshaded (bounded by a corn field and a road) and often exposed to strong winds. Also, the farm pond can dry in some years, but has been dredged, and has a longer hydroperiod (> 1 year). Soils of the area are level and poorly drained (Calsyn et al., 1989). Neither pond contains fish.

Water chemistry and field measurements

Water chemistry and field data were collected from March 15 to June 29, 1997. Water from the ponds was analyzed for total phosphorus (TP), total nitrogen (TN), phytoplankton biomass (as chlorophyll *a*), pH, temperature, and dissolved oxygen (DO). Pond depths and area were also recorded. Temperature and DO data were collected in the field using a YSI, Inc. Model 54 Dissolved Oxygen meter; pH data was collected in the field using a Beckman pH meter. Surface water

samples from the ponds were placed in a cooler on ice and returned to the lab for all other analyses.

Chlorophyll *a* samples were filtered in the lab either the same day or held at 4 °C and filtered the next day. Samples were processed and analyzed according to APHA et al. (1989).

Samples for TP and TN analyses were preserved with 1 ml conc. HCl l⁻¹ sample, and later analyzed. Total phosphorus samples were digested by the persulfate method and analyzed by the ascorbic acid method (APHA et al., 1989). Total nitrogen was analyzed using the digestion procedure and second-derivative spectroscopy of Crumpton et al. (1992).

Life history study

A life history study of the *Daphnia obtusa* from the shaded vernal pond (Woodland) and open farm pond (Farm) was conducted using water from both ponds in a factorial experimental design. Twenty animals from each pond were cultured individually in each of the two treatment combinations.

To start the two laboratory populations of *Daphnia obtusa*, ephippia from each pond were collected from mud samples taken in May 1997. Mud samples were rinsed through a series of sieves with deionized water and examined under a dissecting microscope to remove ephippia. Collected ephippia were placed in vials of fresh deionized water and refrigerated (4 °C) until 800–1000 ephippia had been collected from each pond. The ephippia were then rinsed in fresh deionized water and placed in 250 ml beakers. No food was added to the beakers during incubation of ephippia. The beakers were set under UV-C lights for 20 h and checked approximately every 2 h thereafter until enough neonates were hatched to start the experiment.

The life-history experiment used twenty neonates from each pond (Woodland and Farm ponds). Neonates were placed individually in beakers containing 40 ml of each of two treatments: woodland pond water, or farm pond water. All water used throughout the experiment was sieved (35 μm) and autoclaved to control other possible food sources (e.g., bacteria) in the pond water. All animals were fed trout chow and yeast (TCY), which was made prior to the experiment and frozen, according to Cowgill et al. (1985). Animals were fed 200 ml of thawed TCY every other day, and the water in each beaker was changed every other day to reduce the amount of bacterial growth. Beakers were also covered with plastic wrap to lessen evaporation and contamination by bacteria.

Animals were randomly placed under fluorescent lights (cool white bulbs) on a 12 h light/dark cycle and at an average temperature of 22 °C. Beakers were emptied into a petri dish every other day, rinsed and wiped out with a paper towel, and fresh food and water was added. No algae were found in culture medium by microscopic examination. Each animal was then transferred to a Sedgwick-Rafter chamber and measured for body length, then returned to its beaker. The following variables were also recorded: number of broods; number of neonates; length at first reproduction; final length; and maximum length. Daily observations were continued until all of the animals died. Life-history parameter were calculated using the methods described in Gotelli (1995), and included:

- net reproductive rate R_0 (mean number of offspring produced per female over her lifetime) = $l(x)b(x)$,
- generation time G (average age of parents of all the offspring) = $\frac{l(x)b(x)x}{l(x)b(x)}$,
- intrinsic rate of increase r (rate of population increase) = $(\ln R_0)/G$,

where $l(x)$ = age-specific survivorship, $b(x)$ = age-specific fecundity, and x = age.

Upon culture, we found that two farm pond animals (one in each of two separate treatments) were not *Daphnia obtusa*, but were in fact *Daphnia laevis*; these data were not included in the statistical analyses. In addition, any animals that died before they reproduced were not included in selected analyses (e.g., age at first reproduction), but affected other calculated life history parameters (e.g., R_0 , G , r).

Data were analyzed by ANOVA on either log-transformed or raw values, depending on results of analyses for normality and homogeneity of variance. Analyses were conducted with SAS (SAS Institute, 1984).

Results

Field measurements

The woodland pond had a 69-day hydroperiod (March 13–May 23). After a few days of heavy rain, the woodland pond was again wet for a period of 3 weeks (June 6–June 19) and was dry thereafter. Hydroperiod of the farm pond was ≥ 141 days (we did not observe the pond after July 25). Maximum area of the woodland

Table 1. Summary of ANOVA results for the life history experiment, with treatments of population source, culture water source, and population-water interaction. All variables are expressed per individual female daphnid and/or her broods. NS indicates marginally significant results; see text for further discussion of those results

Experimental treatment	Variable	Significance (P)	Means	
			Woodland	Farm
Population	Age at 1st repro. (days)	0.0005	5.9	5.4
	Size at 1st reprod. (cm)	0.0266	1.74	1.57
	Mean brood size (no. neonates / brood)	0.0001	22.8	17.6
	Total no. of neonates	0.0671 (NS)	219.25	172.9
Water	Mean brood size (no. neonates / brood)	0.0157	21.2	19.0
	Total no. of neonates	0.0552 (NS)	217.9	172.9
	Total no. of nonviable neonates	0.0375	0.4	2.1
	Mean brood size			
Population × water		0.0023	N/A	N/A

pond was 586 m² and mean depth was 28 cm; the area of the farm pond was 1352 m² and maximum depth was 46 cm.

The farm pond was typically warmer, and had greater DO and pH than the woodland pond (Figure 1). The woodland pond was colored by tannic and humic acids, and was virtually anaerobic for much of the hydroperiod.

The farm pond had greater chlorophyll *a* levels on most dates (Figure 1), although the woodland pond also exhibited high chlorophyll *a* values as it dried down. Pheophytin *a* levels in the woodland pond typically exceeded chlorophyll *a* levels, especially just prior to drying. High pheophytin *a* levels were not observed in the farm pond, indicating that high levels in the woodland pond were related to decomposing leaves. The woodland pond typically had greater TP and TN than the farm pond, although one large spike of TP was observed in the farm pond that did not coincide with high levels in the woodland pond (Figure 1). Total nitrogen levels tended to increase as the woodland pond dried; farm pond nitrogen levels remained fairly constant.

In summary, the woodland pond was generally cooler and more nutrient enriched than the farm pond, but had less oxygen and lower pH, and often had less chlorophyll *a* and greater amounts of pheophytin *a* than the farm pond.

Life history study

Daphnia obtusa from the two ponds exhibited different life histories when cultured under identical conditions. Animals from the two ponds were significantly different for the variables: age at first reproduction; size at first reproduction; and mean brood size (Table 1).

Neither the source of animals or water in which they were cultured significantly affected the number of broods. Fifteen of the twenty animals from the woodland pond survived to reproduce when cultured in woodland pond water, and produced an average 9.9 broods/female. All 19 farm pond animals (one animal was identified as *D. laevis*, and was excluded from the experiment) survived to reproduce when cultured in woodland pond water, and produced an average 8.8 broods/female. When cultured in farm pond water, 19 of 20 woodland animals survived to reproduce, and produced an average 8.9 broods/female. Finally, 18 of 19 farm pond animals survived to reproduce in farm pond water (again, one *D. laevis* was excluded), producing an average 9.8 broods/female.

Mean cumulative number of neonates was marginally different between populations ($p = 0.067$). One farm pond animal cultured in woodland pond water lived much longer than other animals and produced 489 neonates during its lifespan. The total number of

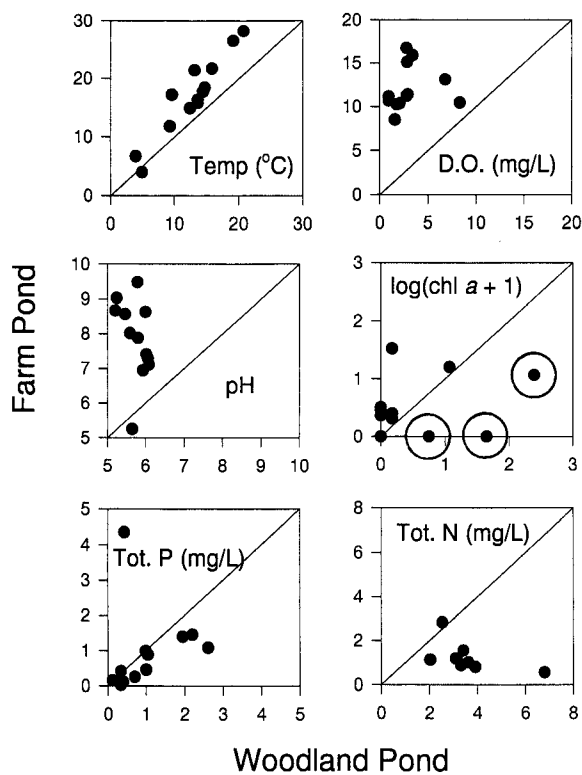


Figure 1. Comparison of environmental variables of the woodland and farm ponds. Each point in all plots represents two measurements collected on the same day. Note that axes are symmetrical for each plot, and the diagonal lines represent identical values in the two ponds. Circled points in the chlorophyll *a* plot were values for the woodland pond after it had dried, and then re-filled, and therefore unavailable as food for *Daphnia obtusa* in the woodland pond.

neonates for this animal exceeded the overall mean +2 standard deviations, but was not a legitimate outlier according to Grubb's test (Sokal & Rohlf, 1981). Therefore, the animal was included in the statistical analysis. As an indication of the effect of this one animal on statistical analyses, data were also analyzed with this animal excluded (as if it was an outlier): in that analysis, the farm and woodland pond populations were significantly different for mean cumulative number of neonates ($p = 0.02$).

The water in which animals were cultured was important for the life history differences between populations (Table 1). The treatments of woodland pond water and farm pond water were significantly different for mean brood size ($p = 0.0157$) and number of nonviable neonates ($p = 0.0375$). In addition, a significant interaction occurred between population source and water source for mean brood size ($p = 0.0023$).

Table 2. Population-level life history variables: generation time (G), net reproductive rate (R_0), and estimated intrinsic rate of increase of the population (r) for all treatments. Values were calculated according to Gotelli (1995)

Population source	Water source	G (days)	R_0	r
Woodland	Woodland	20.4	198.1	0.259
Farm	Woodland	21.1	196.4	0.250
Woodland	Farm	18.9	178.7	0.274
Farm	Farm	18.2	151.9	0.276

In summary, the woodland pond animals started reproducing later than farm pond animals, did so at a larger size, and so had a larger mean brood size, regardless of the water in which they were cultured (Table 1). Also, *Daphnia obtusa* had a larger mean brood size and fewer nonviable neonates when raised in woodland pond water, regardless of the population (Table 1). Finally, the interaction of population and water source significantly affected mean brood size (Table 1).

The effects of population source and water source on individual life history were reflected in population-level life history variables of generation time (G), net reproductive rate (R_0), and intrinsic reproductive rate (r) (Table 2). Farm pond animals grown in their native water had a shorter G and greater r , despite a lesser R_0 , than woodland animals grown in their native water. Both populations cultured in farm pond water had a shorter G and greater r , but lesser R_0 , than when cultured in woodland pond water.

Discussion

As expected, habitats of the *Daphnia obtusa* populations were quite different. The woodland pond was consistently cooler, had much less oxygen and lower pH, more P, more N, and lower concentrations of high-quality food (measured as chlorophyll *a*) than the farm pond. In addition, the two greatest chlorophyll *a* values in the woodland pond occurred when that pond briefly filled again after being dry for 2 weeks. Algae that had been growing on the damp soil may have contributed to greater chlorophyll *a* readings, but these algae were essentially unavailable to the *Daphnia obtusa* population that existed before the pond dried.

These observations suggest that the food for *Daphnia obtusa* in the woodland pond is dominated by

heterotrophs (e.g., fungi, bacteria, flagellates), consistent with other shaded, temporary ponds (Kenk, 1949; Moore, 1970). In contrast, the farm pond has a greater quantity of autotrophic foods that are of greater quality for *Daphnia* (Hall, 1964; Goulden et al., 1982; Tessier et al., 1982; Elendt, 1989; Dodson & Frey, 1991). In summary, the ponds that were the sources for *Daphnia obtusa* and culture water in our life history study differed in multiple ways, with the woodland pond representing conditions that would typically be considered lower quality (physical, chemical and food).

The short hydroperiod of the woodland pond is an indication of an unpredictable habitat: the existence of the habitat is strongly dependent on recent precipitation, and the pond's hydroperiod in 1997 was approximately 2–3 *Daphnia obtusa* lifespans. On the other hand, the farm pond will more predictably provide habitat throughout the interval that a *Daphnia obtusa* population is active. Consistent with Stearns' (1976) expectations (also see Stearns, 1992), *Daphnia obtusa* from the unpredictable woodland pond used a mixed life history strategy in comparison to *D. obtusa* from the farm pond. Woodland pond animals were slightly older, and therefore larger at first reproduction; traits that, at first glance, may seem deleterious in an unpredictable habitat. However, those modest differences enabled animals to produce larger broods and more offspring, which compensated in part for delayed reproduction and could ultimately increase the number of ephippia produced when the pond dries.

Relatively low survivorship in the woodland pond may select for greater R_0 in the woodland population. Given that food quality is relatively poor in the woodland pond, and that larger animals are more efficient filter-feeders than smaller animals (Lampert & Sommer, 1997), reproductive output may be better attained by delaying reproduction until animals are larger and can more efficiently feed and produce larger broods. Conversely, farm pond animals may be less constrained by poor food quality, and reproduce earlier (smaller) in their life cycle.

However, life history variables were also affected by the source water used for culture. Both populations had larger broods and fewer nonviable neonates when cultured in woodland pond water than in farm pond water, and the effect was greater for farm pond animals than woodland pond animals. This translated to longer generation times, and slower population growth rates, but more offspring per individual in woodland water than farm pond water. Unanalyzed chemical differences (e.g., dissolved organic compounds), including

the possibility of microbial growth on dissolved organics, may have contributed to differences in *Daphnia obtusa* life history between water sources. It is possible that dissolved organic compounds in woodland temporary ponds benefit *Daphnia obtusa* reproduction and contribute to the success of these animals in unpredictable environments. This effect of source water would not be apparent in a simpler common-garden experimental design (e.g., using reconstituted hard water), nor by comparing life history traits among populations based on samples collected in the field.

Several life history studies on *Daphnia* spp. have been conducted (e.g., Slobodkin, 1954; Hall, 1964; Vanni, 1987). Vanni's (1987) study most closely resembled our study: he compared life history traits of 7 *Daphnia pulex* genotypes, including several from central Illinois. The objective of Vanni's (1987) study was to compare colonization abilities of 7 genotypes in 2 permanent waters (a eutrophic pond and an oligotrophic lake), assuming simultaneous arrivals. Vanni (1987) compared life histories of 4 genotypes from temporary woodland ponds, 2 from permanent farm ponds, and 1 genotype from a permanent lake in Michigan. The life history experiments were conducted in a laboratory, with each genotype raised in each of the two filtered (44 μm) waters. Food was unidentified phytoplankton and bacteria in the filtered water, which was replenished every 2–3 days. In general, the eutrophic pond water provided more abundant food resources than the oligotrophic lake water. Vanni raised *Daphnia* for 2 generations, with the second generation used to collect life history data, and noted that one of the temporary woodland pond species more closely resembled *D. obtusa*, the species used in our study.

We compared life history traits for *D. obtusa* in our study (a dystrophic woodland pond and a eutrophic farm pond) with Vanni's (1987) results. We excluded Vanni's (1987) permanent lake population from our comparisons, but did include populations from permanent farm ponds:

(1) Size at first reproduction. Vanni (1987) found most genotypes from temporary woodland ponds were smaller than the farm pond genotypes, regardless of culture water (Table 3). Most genotypes began reproduction at a smaller size in eutrophic lake water than in oligotrophic lake water. In contrast, we found that the woodland pond animals began reproduction at a larger size than the farm pond animals, and both populations were larger in size at first reproduction in woodland pond water than in farm pond water (Table 3). The

Table 3. Comparison of life history data from Vanni (1987) and this study. Values are ranges of mean data for each population type for Vanni (1987) and actual means for this study. Vanni used 4 ephemeral pond populations and 2 farm pond populations, each cultured in either oligotrophic (O) or eutrophic (E) water. Our study cultured animals from a woodland (W) and a farm (F) pond in both kinds of water

Variable	Vanni (1987)			This study		
	Water	Populations		Water	Populations	
		Ephemeral	Permanent farm pond		Woodland	Farm pond
Size at 1 st reprod.	O	1.41–1.77	1.61–1.74	W	1.79	1.60
	E	1.39–1.55	1.61	F	1.69	1.53
Age at 1 st reprod.	O	6.22–6.87	7.22–7.50	W	5.73	5.42
	E	5.60–6.78	6.00–6.75	F	6.00	5.30
Size of 1 st brood	O	3.75–4.78	4.00–5.10	W	11.20	9.79
	E	6.80–8.22	8.25–8.43	F	10.00	10.22
Size of 2 nd brood	O	1.22–6.10	1.40–5.56	W	20.11	15.18
	E	9.11–14.75	14.25–14.43	F	19.67	17.82

range of sizes at first reproduction in our study was similar to that of Vanni (1987).

(2) Age at first reproduction. All genotypes began reproducing earlier in eutrophic lake water of Vanni's study (Table 3). Similarly, we found that both populations began to reproduce earlier in farm pond water. In Vanni's study, all ephemeral populations were younger at first reproduction than farm pond populations in oligotrophic water, but in eutrophic water the data were mixed. In our study, woodland pond animals were older at first reproduction than farm pond animals in both water types (Table 3). Ages at first reproduction were similar to those of Vanni (1987).

(3) Brood size. Vanni (1987) recorded brood sizes, but only for the first two broods released. Populations from temporary ponds produced fewer offspring than the farm pond populations in eutrophic water, but results were mixed in oligotrophic water (Table 3). All genotypes produced larger broods on eutrophic pond water than on oligotrophic lake water. Brood size increased with the second brood in eutrophic lake water, but not in oligotrophic water. In our study, brood size was nearly the same for the two populations in the first brood, but the woodland population had a larger second brood. Each population produced larger broods in its own water, and brood size increased between broods in all cases (Table 3).

(4) Rate of increase. All of Vanni's (1987) populations had higher rate of increase (F_n) in the eutrophic water than in the oligotrophic water. Populations from

temporary ponds generally had higher F_n than the farm pond populations in the oligotrophic water treatment, but F_n values were mixed in eutrophic water. In our study, intrinsic rate of increase (r) was greatest for the farm pond population, but each population had its greatest rate of increase in water not its own, reflecting earlier reproduction.

Vanni (1987) attributed differences in life history measurements between lake waters to the greater resource supply (i.e., more phytoplankton) in the eutrophic lake water. The provided food resources in our study were identical (trout chow and yeast) across pond water treatments, and would usually be considered of inferior quality compared to the food resources from either pond in Vanni (1987). It is possible that dissolved organic matter in woodland pond water enhanced nutritional quality and/or quantity of microbial food in our study, but it is not that simple: animals had larger broods in woodland pond water, but did not grow faster. Also, we think it is interesting that our woodland pond population, raised on trout chow and yeast in its own water, performed as well or better than the populations from temporary ponds of Vanni's (1987) study, especially in brood size.

Examination of our results, and comparisons to the work of Vanni (1987), suggest that substantial variation in life history traits exists among local and regional populations. Life history traits were expressed differently in experimentally-similar conditions in both our study and that of Vanni (1987).

Different life histories under similar conditions could result from populations that have different tolerance ranges, and may indicate limits to phenotypic plasticity in *Daphnia* (Lynch & Gabriel 1987).

Local selection is commonly thought to result in different life histories of *Daphnia* populations (Lampert & Sommers, 1997). A temporary woodland pond is a fluctuating, unpredictable habitat (Stearns, 1976) with stringent physical/chemical conditions. Woodland pond *Daphnia obtusa* have adapted well to these conditions, and to foods that would be considered low-quality for other *Daphnia* species from other habitats. If animals from such a pond had been used in comparative studies of food quality for *Daphnia*, rather than *Daphnia* from permanent waters (Hall, 1964; Goulden et al., 1982; Tessier et al., 1982; Keating, 1985), trout chow and yeast might not have been considered a poor-quality food for culture.

We can most readily ascribe local selection as the cause of population divergence when populations are not otherwise separated, as by limited dispersal among populations. If dispersal is rare among isolated temporary ponds, then differences among populations may also result from persistent founder effects (Boileau et al., 1992), in addition to effects of local selection. *Daphnia* and other zooplankton are commonly thought to disperse readily among aquatic systems (e.g., Lampert & Sommer, 1997), but some recent studies indicate otherwise (Jenkins, 1995; Jenkins & Buikema, 1998; Jenkins & Underwood, 1998). Therefore, further studies on the relative importance of local (i.e., selection) and regional (i.e., dispersal) processes will best discern the mechanisms causing differences among populations. Life histories should provide a valuable perspective for these important ideas in aquatic ecology.

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