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THE MIDSUMMER DYNAMICS OF TWO DAPHNIA SPECIES IN WINTERGREEN LAKE, MICHIGAN

Ву

Stephen Thomas Threlkeld

A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

ABSTRACT

THE MIDSUMMER DYNAMICS OF TWO DAPHNIA SPECIES IN WINTERGREEN LAKE, MICHIGAN

By

Stephen Thomas Threlkeld

Midsummer reductions in densities of Daphnia populations are common and have been reported worldwide. During 1976 reductions were also found for Daphnia pulicaria and Daphnia galeata mendotae populations in Wintergreen Lake, Michigan. Previous attempts to determine the causes of such declines have indicated correlations between predator populations, the presence of unpalatable algae or high midsummer water temperatures, and the reduction or disappearance of the daphnid populations. In this study, in situ life table experiments were performed to assess the influence of natural food and temperature conditions on population growth. The effect of predation by fish and Chaoborus was assessed by analysis of population size structure, predator gut contents, recovery of sedimented fecal material, and the age distribution of parthenogenic eggs carried by the females of the population.

A weekly sampling program showed that <u>D</u>. <u>pulicaria</u> was dielly concentrated after early summer at depths between the anaerobic hypolimnion and the warmer epilimnion, consistent with previous information indicating it to be a cold-water species. However, in situ life table data showed that <u>D</u>. <u>pulicaria</u> was capable of surviving in epilimnetic water up to 27°C, although reproduction was greatly reduced for a six day period in mid-July. This reduction in reproduction appeared to be the result of an interaction of high temperatures, declining standing crops of small algae and increasing amounts of <u>Anabaena, Ceratium</u> and <u>Volvox</u>. <u>D</u>. <u>galeata mendotae</u> did not show any adverse effect due to these mid-July algaetemperature conditions.

Analysis of predator gut contents suggested that both daphnids were heavily preyed upon by bluegills (<u>Lepomis macrochirus</u>). Shifts in the size structure of the daphnid populations were also consistent with intense size-selective predation by bluegills, as was the tendency for the age distribution of parthenogenic eggs to become skewed to younger eggs as the decline proceeded. Differences in body size, epphipial production, and habitat preferences between the two species are also consistent with the hypothesis that planktivory is a strong selective force in their evolution.

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INTRODUCTION

Seasonality is common to all natural ecological To the extent that seasonal changes in abiotic systems. and biotic aspects of natural environments are predictable, natural populations evolve life history characteristics (e.g., habitat preferences, reproductive strategies, body size) which permit them to persist under temporary conditions unfavorable for continued population growth. Factors important in the seasonal fluctuations of natural populations must play an important role in the evolution of these life history characteristics. Although identification of selective pressures and the evolution of life history tactics in terrestrial plants and animals has become a major focal point in contemporary ecology, the relationship between population regulation and life history evolution of planktonic organisms has not yet been adequately addressed. The major impediment to this synthesis in aquatic systems has been difficulty in the unequivocal identification of factors most important in seasonal population regulation.

For example, although midsummer declines of Daphnia populations have been reported worldwide (e.g.,

Birge 1896, Hall 1964, Wright 1965, Clark and Carter 1974, DeBernardi 1974, George and Edwards 1974, Fott 1975) no consensus exists on what is their cause. A number of hypotheses which have been proposed for such midsummer declines of Daphnia are summarized in Table 1. Basically these hypotheses may be classified as those related to (1) increased water temperature, (2) changing food conditions, (3) increased activity or abundance of invertebrate predators (e.g., Chaoborus, Leptodora), and (4) increased activity or abundance of vertebrate predators (various fish species). Whether a general combination of these factors regulates the midsummer abundance of all Daphnia species or not is unknown. However, of the four classes of factors cited in Table 1, usually three or more are associated with each of the reported declines. The multiplicity of hypotheses for each species' dynamics has made thorough analyses difficult, and those without independent assessments of each hypothesis unconvincing. Thus, it is impossible to evaluate how important various behaviors, allocations of energy between reproduction and growth, or habitat choices are in permitting species populations to persist in aquatic systems.

The present study attempts to combine an analysis of the midsummer decline of two <u>Daphnia</u> species (<u>D. puli-</u> <u>caria</u> Forbes and <u>D. galeata mendotae</u> Birge) in Wintergreen Lake, Michigan, with an evaluation of factors influencing

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Table 1. Major hypotheses for the midsummer decline of Daphnia populations.

Hypothesis	Decline mediated by	Reference
Increased water temperature	Restriction of vertical distribution to deeper, cooler waters	Birge 1895, 1896, Hall 1964, Tappa 1965, Bell and Ward 1970, Haney and Hall 1975
	Degeneration of parthenogenic eggs	Hrbáčková-Esslová 1962
	Increased mortality	Craddock 1975, Goss and Bunting 1976
	Decreased assimilation efficiency	Lampert 1977
	Decreased filtering rate	Burns 1969
Changing food conditions	Curtailment of individual growth and increased vulnerability to invertebrate predators	Hall et al. 1976
	Filtering rate inhibition	Crowley 1973
	Decreased assimilation efficiency	Nowak 1975
	Reproductive decline	George and Edwards 1974, Clark and Carter 1974, Kwik and Carter 1975
	Increased mortality due to: starvation toxicity of midsummer algae pH extremes resulting from increased photosynthesis	Threlkeld 1976 Arnold 1971 O'Brien and DeNoyelles 1972
Invertebrate predators	Increased mortality associated with: increased abundance of predators	Wright 1965, Hall 1964, DeBernardi 1974
	increased activity (related to water temperature or predator growth)	Fedorenko 1975
Vertebrate predators	Increased mortality associated with increased abundance and individual feeding activity (temperature or growth related) of predators	Hrbáček 1962, Galbraith 1967, Noble 1975, Clark 1975, Fott 1975, Fott et al. 1974, Baumann and Kitchell 1974, Wong and Ward 1972, Ward and Robinson 1974

the life history characteristics and midsummer distribution of these two species in north temperate lakes.

METHODS AND MATERIALS

構成で

Wintergreen Lake is a small (15 ha, max. depth 6.3 m, average depth 3.5 m), hypereutrophic lake in southwestern Michigan located on the Kellogg Bird Sanctuary of the Kellogg Biological Station of Michigan State University (Manny 1972, Manny et al. 1977, Wetzel 1975, Wetzel et al. unpubl. data). Vast amounts of nutrients are introduced into the lake by migratory and resident bird populations which result in an annual mean primary productivity greater than 1200 mg C \cdot m⁻² .day⁻¹ (Manny 1972, Manny et al. 1975). Common midsummer algal genera include Aphanizomenon, Anabaena, Ceratium, and Microcystis (Manny 1972, Crowley 1973); midsummer water transparency (Secchi disk) is usually less than 1.0 m (Wetzel 1975, Wetzel et al. unpubl. data, Klug et al. unpubl. data). Approximately 50% of the surface area of the lake is covered with floating and submergent vegetation (Nuphar, Nymphaea, Potomageton, Hydrodictyon). All limnological measures except where otherwise noted were obtained from a single station located in the deepest, limnetic region of the lake (A in Figure 1).

Figure 1. Bathymetric map of Wintergreen Lake showing sampling stations used in this study. The distribution of macrophytes is indicated by the shading. Contour intervals are shown in meters.

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Figure 1

ELEVATION 271m, AREA 15 ha

Estimates of the amount and quality of food available to zooplankton in Wintergreen Lake were based on measurements of: (1) chlorophyll a and phaeopigments, and (2) algal size structure and taxonomic composition. Piqment analyses were performed on particulate matter collected biweekly at 1-meter depth intervals. Water samples were filtered through Millipore filters (HA, 0.45 µm), plant pigments extracted in 90% aqueous acetone and absorbances read using a Hitachi Perkin-Elmer Model 139 Spectrophotometer. Following acidification with 1 N HCl the samples were read again. Chlorophyll a and phaeopigment concentrations were calculated from the absorbance equations of Wetzel and Westlake (1969). Algae, collected each week from 1-meter depth intervals, were preserved in Lugol's solution. Algal samples from the surface meter (0.5 m) taken from June 15 to August 3 were analyzed for size structure using a Model A Coulter Counter. In addition, July algal samples were settled and viewed with a Wild Inverted microscope; identifications were made according to Prescott (1970).

Physical and chemical parameters measured each week included pH, dissolved oxygen (Winkler technique), water transparency (Secchi disk), and temperature (YSI thermistor). Temperature was measured each day during the summer months (June-September).

Zooplankton were collected by two methods. Once a week, the vertical distribution and abundance of Daphnia was assessed by taking duplicate 4-liter Van Dorn samples at 1-meter depth intervals at both noon and midnight. Also, vertical tows with a 15-cm diameter, 145-um mesh net were taken each week at midnight in triplicate at Station A and in duplicate on a biweekly schedule at three peripheral stations (B, C, and D in Figure 1). From July 10-31 duplicate vertical tows were also taken each day in midafternoon at Station A. All zooplankton were collected and concentrated on 145- μ m mesh netting. Preservation in 4% sucrose (40 g/liter) formalin solution (Haney and Hall 1973) prevented the loss of Daphnia eggs and distortion of the carapace by ballooning.

Analysis of vertical tow samples from Station A involved taking sufficient 1-ml aliquots from the sample jars (50-100 ml) to count at least 200 individuals of each <u>Daphnia</u> species present. <u>Daphnia</u> were counted in a Petri dish modified with plastic baffles to serve as a Bogorov plankton counter (Gannon 1971), thus eliminating any remixing and accidental recounting of individual animals. In addition, the carapace length (exclusive of tail spine and head) of each of the 200+ individuals was measured to within 0.1 mm (0.2 mm size classes) and the number of eggs and their stage of embryonic development was noted. The stages of development of Daphnia

parthenogenic eggs were identified according to criteria in Table 2, modified from Green (1956), Lei and Clifford (1974), and George and Edwards (1974).

Displacement volumes of midnight vertical tow collections of plankton from stations A, B, C, and D were measured in a graduated cylinder after removal of the preservative solution by filtration. Aliquots containing 100 or more Daphnia were also examined to see if the relative abundance of species was consistent between stations. Van Dorn samples were counted in their entirety for total individuals, parthenogenic eggs, gravid females, males and epphipial females for each Daphnia species present. Egg ratios (Edmondson 1974) were calculated for all Station A samples by dividing the number of parthenogenic eggs present by the total number of females. References for zooplankton identification were: Daphnia pulicaria (Brandlova et al. 1972, Hrbáček 1959), D. galeata mendotae (Brooks 1957), Chaoborus punctipennis (Saether 1972), all other zooplankton (Edmondson 1957).

Fish were collected by gill net and hook and line, primarily in the limnetic zone of the lake. Stomachs were removed and preserved in 4% sucrose-formalin solution. From July 12-30, sedimenting seston was collected by duplicate glass jars (6.25 cm diameter, 12.5 cm depth) suspended at 4.5 m. The jars were collected daily and replaced with clean jars; the contents were concentrated

Stage	Description	Relative Duration (Percent of total ± 2.0 std. errors)	References ^a
1	Egg stage, egg membrane intact; no differentia- tion into body regions	30.2 ± 2.2	LC I, II; GE I; G I, II; OF 1-4; E 1-3
2	Embryo with or without head bulge; antennae becoming distinct; eye spots not yet visible	32.0 ± 1.4	LC III, IV; GE II; G III, IV; OF 5-7; E 4-5
3	Embryo with two small pink or red eyes	8.7 ± 0.5	LC V; GE III; G V, VI; OF 8; E 6
4	Embryo with two brown or black eyes	13.0 ± 0.5	LC VI, VII; GE IV; G VII
5	Embryo with a single median black eye	16.0 ± 2.7	LC VIII; G VIII $\begin{cases} OF & y = 13 \\ E & 7-8 \end{cases}$

Table 2. Criteria for ageing parthenogenic eggs and percent of total development time spent per stage.

^aLC: Lei and Clifford (1974); GE: George and Edwards (1974); G: Green (1956); OF: Obreshkove and Fraser (1940); E: Esslová (1959). Roman numerals refer to egg stages and arabic numerals to figures in the literature cited. 11

on 145-µm netting and preserved in 4% sucrose-formalin solution. Analysis of these samples was limited to assessing the relative numbers of <u>Daphnia</u> found in undigested and digested states (in fish fecal material); degradation of zooplankton chitin was not observed over the brief (<1 day) period the material may have remained in the collecting jars.

In addition to the Wintergreen Lake studies, nine other lakes (Table 3) in southwestern Michigan of different depth and water transparency were sampled in August, 1976, to assess diel vertical distribution of any <u>D</u>. <u>pulicaria</u> and <u>D</u>. <u>galeata mendotae</u> present. Duplicate vertical net tows (15-cm diameter, $145-\mu m$ mesh net) were taken during the day and at night in the epilimnion and the entire water column. Hypolimnion-residing zooplankton were estimated by taking the difference between numbers collected in the epilimnion and in the total water column; these numbers and tow volumes were then used to calculate mean densities per liter of these species in the epilimnion and hypolimnion.

Lake,	Maximum Depth (m)	Secchi Disk (m)	Surface Alkalinity (mg CaCO ₃ /1)	Temperature	Mean Number per Liter				
Date Sampled				Range (°C)	<u>D. pulicaria</u>	D. galeata mendotae			
				***********	(D) (N)	(D) (N)			
Bassett 16-VIII-76	9.5	2.9	143	(E) 20.8-21.5 (H) 9.0-20.8	0.6 0.0 4.4 6.6	36.2 171.2 10.9 40.7			
Deep 16-VIII-76	9.0	5.0	149	(E) 21.4-22.0 (H) 10.2-21.4	0.0 0.4 11.3 3.9	16.4 126.2 8.7 0.0			
Hamilton 18-VIII-76	11.0	3.0	198	(E) 21.5-22.9 (H) 6.3-21.5	0.0 0.9 2.4 5.3	2.5 33.3 2.6 2.2			
Lawrence 20-VIII-76	12.0	3.5	194	(E) 21.4-23.2 (H) 8.3-21.4	0.0 0.9 6.3 5.3	10.4 53.1 6.5 0.0			
Little Mill 20-VIII-76	8.0	4.4	154	(E) 22.6-23.8 (H) 9.5-22.6	0.0 0.8 11.3 7.1	17.5 84.0 35.9 0.0			
MacDonald 16-VIII-76	3.2	3.2	135	(E) 21.7-22.3	not present	not present			
Palmatier 18-VIII-76	10.0	4.2	176	(E) 20.5-22.2 (H) 8.3-20.5	0.0 0.3 1.2 2.7	26.3 51.4 0.0 0.0			
Three Lakes 20-VIII-76	8.0	4.5	165	(E) 21.8-23.7 (H) 12.0-21.8	not present	11.5 34.4 5.8 0.0			
Warner 18-VIII-76	15.0	5.0	115 _	(E) 20.9-22.5 (H) 5.0-20.9	0.0 0.0 2.5 3.3	36.9 71.3 0.0 0.0			

Table 3. Mean number of <u>Daphnia pulicaria</u> and <u>D. galeata mendotae</u> per liter in the epilimnion (E) and hypolimnion (H) of nine southwestern Michigan lakes during the day (D) and at night (N) in August, 1976.

GENERAL POPULATION DYNAMICS

Four data sets were available for the study of the midsummer population dynamics of the two Daphnia species in Wintergreen Lake, resulting from noon and midnight Van Dorn collections and from vertical tow samples taken at midnight and from July 10-31 in midafternoon. The average coefficient of variation between subsamples from vertical tow collections was 21.7%, and 26.7% between the replicated tow net samples. The average coefficient of variation between replicate Van Dorn samples (depth and time specific) was 28.0%. In contrast to these relatively low coefficients of variation within sampling regimes, the variation between estimates derived from different regimes was substantial, amounting to 50.8% between day and night estimates derived from Van Dorn samples, 63.8% between day and night estimates from vertical tow samples, and 73.6% among all sampling regimes. Substantial variation is expected among collections made with different devices and at different times of the day (Langeland and Rognerud 1974, Smyly 1968, Szlauer 1964, Hodgkiss 1977). In spite of this variation, the

different sampling regimes concur in the timing and precipitous nature of the decline (Figure 2). That this decline occurred in a similar fashion on a lake-wide basis was confirmed by examining zooplankton collected at stations B, C, and D.

Daphnia pulicaria appeared shortly after spring overturn (Figures 2, 3, and 4), hatching from epphipia. The population increased throughout April, reaching its maximum density in early May. Production of males and resting eggs (epphipia) occurred from early May until mid-June. Since only parthenogenic eggs were included in the calculation of the egg ratio, a sharp decline in the egg ratio was expected and observed during this period (Figure 2). Following the disappearance of males and epphipia-bearing females in June, a residual population resumed active parthenogenic reproduction, although the egg ratio showed a steady decline until late July when the population disappeared altogether.

<u>D. pulicaria</u> was generally found at depths where water temperature did not exceed 22°C and where oxygen was present (Figure 4). There was little diel vertical migration of this population to warm epilimnion waters (Figure 4).

Daphnia galeata mendotae did not appear until June, but increased dramatically thereafter. After reaching its peak density in mid-July this population

Top panel: Mean number of Daphnia pulicaria Figure 2. (----) and D. galeata mendotae (---) per liter as estimated by noon (o) and midnight (\bullet) Van Dorn collections and by midafternoon (\Box) and midnight () vertical tow collections. For graphical clarity, Van Dorn and midnight vertical tow records are terminated on the last date each species was observed in those samples. The last date each species was observed in midafternoon vertical tows is indicated by a P (for D. pulicaria) or G (for D. galeata mendotae) on the abscissa. Bottom panels: Mean number of parthenogenic eggs per female D. pulicaria and D. galeata mendotae as estimated by four sampling regimes; symbols as used in top panel.





Figure 3. Depth-time distribution of isopleths of temperature (°C) (top panel) and dissolved oxygen (mg liter⁻¹) (bottom panel).

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Figure 4. Depth-time distribution of isopleths of <u>Daphnia pulicaria</u> per liter at noon (top) and midnight (bottom). Water depths without oxygen and greater than 22°C are indicated by stipling and shading, respectively, in the lower panel.



disappeared in late July (Figures 2 and 5). The three weekly sampling regimes (midnight and noon Van Dorn samples, midnight vertical tows) did not provide sufficient resolution of the rapidity of this species' decline; the vertical tow samples collected each day in midafternoon during July showed that this decline was extremely rapid and spread over a twelve day period (Figure 2). The egg ratio of <u>D</u>. <u>galeata mendotae</u> declined throughout July suggesting the importance of changing food conditions in their late July disappearance. This species was concentrated in the metalimnion during the day, but became more dispersed in the epilimnion at night (Figure 5).

Figure 5. Depth-time distribution of <u>Daphnia galeata mendotae</u> per liter at noon (top) and midnight (bottom).



IN SITU LIFE TABLE EXPERIMENTS

Basic to a discussion of a causal link between a declining egg ratio and a declining population is the assumption that some source of mortality is offsetting the remaining reproduction occurring in the population. In previous studies of the midsummer dynamics of various zooplankton species (Hall 1964, Wright 1965, DeBernardi 1974, Kerfoot 1975, Kwik and Carter 1975), the instantaneous rate of mortality d has been estimated by the difference equation, r = b-d, where r is the observed rate of population change and b is the instantaneous birth rate (based on egg ratio and development time information: see Caswell 1972, Paloheimo 1974, Edmondson 1974). Past interpretations that changes in d resulted from changes in predator-related mortality rest on the assumption that physiological mortality did not change during the period over which r and b were estimated, and that shifts in the age structure of the population did not result in biased estimates of birth rate. In this study a series of in situ life table experiments was performed to assess the predator-free, age-specific
response of both <u>Daphnia</u> species to natural food and temperature conditions from June 17 to September 12, 1976. This information provided a means of calculating population growth rate and time- and age(size)-dependent physiological mortality.

Methods and Materials

Each life table experiment was started from individual female Daphnia isolated from Wintergreen Lake water during this period and incubated (at Station A, see Figure 1) in a 75-ml clear glass jar with screw cap and placed at 0.5 m, 2.5 m, 3.0 m, or 3.5 m. Such females and all other cohorts derived from them were incubated in lake water collected at the same depths the jars were suspended and filtered through a 145-um mesh net to remove other zooplankton. When the brood females gave birth, they were removed and discarded, and the life history characteristics (survivorship, growth, reproduction) of their offspring were followed until all members of the cohort were dead or until September 12, when all remaining cohorts were terminated. During the life of the cohort members, newborn individuals were removed and used to start other cohorts or discarded.

Animals were transferred daily by wide-bore pipette to clean jars and freshly collected water, and returned to their in situ incubation depths within two hours of their removal from the lake. This daily

transfer procedure permitted a constant renewal of water and algae as the animals might experience in the lake (minus predation). In addition, the transfer period permitted daily assessment of the survivorship, reproduction and growth of the members of each cohort. Survivorship was measured by counting the number of live animals during transfer to the clean jars; collection of dead individuals at the bottom of the previous day's jars provided a check on these daily survivorship counts. Reproduction was measured during the daily removal of newborn individuals (easily distinguishable from adults by size). In addition, any dead newborn individuals were collected from the bottom of the jars and eggs cast off in undeveloped condition with the molts were counted. Individual growth was assessed by measuring the molts (exclusive of tail spine) discarded during the previous day's incubations. The response of daphnids to different food conditions throughout the summer was assessed by continually starting new cohorts (and thus having several cohorts of different age present on any date in the summer); and the entire set of cohorts provided a means by which the difference between daphnid response to natural conditions with and without predators might be assessed.

In addition to the assessment of survivorship, growth and reproduction by animals in water from depths normally inhabited by them in the lake, animals were also

incubated in 0.5 m water at a depth of 4.5 m after the freshly collected surface water had been cooled to temperatures at 4.5 m. This particular manipulation provided a measure of the effect of temperature (where food conditions were identical) on life history characteristics of these species. As in the epilimnion (0.5 m) and metalimnion (2.5 m, 3.0 m, 3.5 m) experiments, incubations using 0.5 m water at 4.5 m were started on several dates during the summer to evaluate the effect of seasonal changes in natural food conditions. The life history characteristics of over 250 cohorts of the two species were determined during the period June 17-September 12.

Information from these cohorts was combined according to cohort starting date and depth of incubation to give age-specific survivorship (1_x) and reproduction (m_x) schedules for each species. Survivorship and reproduction were then used to calculate population (cohort specific) growth rate r (hereafter, cohort r), where $\Sigma \ 1_x m_y e^{-rx} = 1.0$ (Lotka 1945).

Cohort densities were determined by the number of offspring produced per brood by the isolated brood females, and ranged from 1 to 10 animals/75 ml jar (13.3 to 133.3/liter). Initial cohort density did not significantly affect cohort r on several test dates during the summer, presumably because the rates of exploitation of food in the water at these densities

were sufficiently low compared to the 100% replacement of water per day. Population growth rate generally decreases (Frank, Boll and Kelly 1957) or remains constant (as in present results) with increasing cohort density. Since the initial cohort densities in the in situ life table experiments were greater than or equal to <u>Daphnia</u> densities in the lake, they should, therefore, tend to provide conservative estimates of their growth capabilities under natural conditions.

Results and Discussion

Population growth rates (r) calculated from the cohort experiments were much higher throughout the summer than anticipated from the observed dynamics of the two <u>Daphnia</u> species in Wintergreen Lake. All cohorts of <u>D. pulicaria</u> started during the period June 17-September 12 were able to replace themselves ($r \ge 0$) and, in general, r values exceeded 0.1 (day⁻¹). Similarly, <u>D. galeata</u> <u>mendotae</u> showed positive r values throughout the summer with the exception of three cohorts incubated at 3.5 m in early July. The natural population of <u>D. galeata</u> <u>mendotae</u> survived longer than the members of these three cohorts, and all other cohorts of this species (n = 58) were capable of replacing themselves. Thus it appears that the natural milieu was suitable for the continued growth of both species throughout the summer.

Figure 6 shows that cohort r of D. pulicaria in epilimnion and metalimnion incubations was depressed in Separate analyses of $l_{\mathbf{x}}$ and $\mathtt{m}_{\mathbf{x}}$ data (according mid-July. to Keyfitz 1968) showed that changes in age-specific survivorship from June to July only accounted for about 4% of the reduction in cohort r during this period. In contrast, about 75% (the remaining 21% being due to interaction) of the observed reduction in cohort r was associated with an age-independent reduction in reproduction for a six day period in mid-July (Figure 7). Cohorts begun shortly before or during this period thus took longer to begin reproduction, and cohort r was thus substantially reduced. The mid-July food and temperature conditions associated with this reduction in reproduction will be discussed later. In spite of this reproductive slowdown, individual growth was not slowed during this period. The size structure of the natural population during mid-July shows a gradual elimination of small-bodied individuals probably caused by reduced recruitment as seen in the life table experiments coupled with continued growth of existing juveniles into larger size classes (Figure 8). The successive elimination of large size classes shown in Figure 8 is unaccounted for by mortality estimates from the in situ life table experiments.

The presence of egg-bearing individuals in the natural population (Figures 2 and 8) in mid-July appears

Figure 6. Isopleths of population growth rate (cohort r) for cohorts of <u>Daphnia</u> <u>pulicaria</u> as a function of the date the cohorts were started and the mean water temperature experienced by the cohort's individuals prior to maturation. Epilimnion incubations are indicated by closed circles (●), metalimnion (2.5 m, 3.0 m, 3.5 m) incubations by open circles (O), and hypolimnion incubations by closed squares (■).

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Figure 7. Age-specific reproduction (m_x) of <u>Daphnia pulicaria</u> cohorts incubated at 0.5 m.

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Figure 8. Size structure of <u>Daphnia pulicaria popu-</u> lation during July, 1976. The solid vertical line indicates the minimum size of reproductive individuals in the population; shaded areas indicate egg-bearing females. 36 D. pulicaria

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BODY SIZE

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to contradict the near-total elimination of reproduction observed at the same time in the life table experiments. During mid-July some eggs did appear in animals in the life table experiments but they were largely aborted with the cast molts (Figure 9); the eggs appeared quite normal and would have been included in an egg ratio calculation from a natural sample.

In contrast to <u>D</u>. <u>pulicaria</u>, cohorts of <u>D</u>. <u>galeata</u> <u>mendotae</u> did not show any decline in cohort r in epilimnion incubations in mid-July (Figure 10). An analysis of the size structure of the <u>D</u>. <u>galeata mendotae</u> population during its late July decline strongly suggests that sizespecific mortality of reproductive individuals was responsible for its elimination, as the larger size classes were successively removed from the natural population as the decline proceeded (Figure 11). This mortality cannot be explained by natural physiological mortality as measured in the life table experiments.

The declining egg ratio of the natural population of <u>D</u>. <u>galeata mendotae</u> (Figure 2) during this period does not appear to be consistent with the continued ability of cohorts in the life table experiments to grow at r values of 0.15 to 0.3 (Figure 10). This apparent discrepancy is resolved by noting the removal of large-bodied, eggbearing females from the natural population during this period. Because the elimination of larger size classes

Figure 9. Daily egg production (eggs.adult female alive-1. day-1) by Daphnia pulicaria in in situ life table experiments at all incubation depths. Shaded areas indicate eggs which were cast off in undeveloped condition with molts; open areas indicate live births. No cohorts were started at 3.5 m after mid-July.

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DAILY EGG PRODUCTION

Figure 10. Isopleths of population growth rate (cohort r) for cohorts of Daphnia galeata mendotae as a function of the date the cohorts were started and the mean water temperature experienced by the cohort's individuals prior to maturation. Symbols as in Figure 6. The three cohorts from 3.5 m having negative r values (see text) are omitted.



Figure 11. Size structure of Daphnia galeata mendotae population during July, 1976. Format as in Figure 8.

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.4 .6 .8 1.0 1.2 1.4 1.6



Figure ll

is so rapid in late July (the maximum size of <u>D</u>. <u>galeata</u> <u>mendotae</u> decreases from 1.8 mm to 0.8 mm in two weeks) the contribution of parthenogenic eggs by larger individuals is reduced more rapidly than the remainder of the population can re-establish a stable age-size structure. The constancy of the relationship between brood size and body size (Figure 12) throughout this period supports the idea that the observed decline in the egg ratio of the natural population is not due to inadequacy of the natural food supply. It appears that the slope of the brood sizebody size relationship is less sensitive to rapid transitions in the age or size structure of the population than is the traditional egg ratio calculation, and may be preferable as an indicator of population growth potential.

The decline of both <u>Daphnia</u> populations in Wintergreen Lake is associated with adult mortality in excess of that observed in the in situ life table experiments. This mortality appears to be size-selective as larger size classes are eliminated prior to the removal of smaller ones. In addition, in the decline of <u>D</u>. <u>puli-</u> <u>caria</u>, juvenile size classes show a disproportionate loss due to continued individual growth and reduced reproduction by adults.

Figure 12. Brood size-body size relationships for Daphnia galeata mendotae population during July, 1976. Vertical bars include the mean ± one standard deviation.

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Figure 12

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POPULATION LOSSES

Many of the hypothesized adverse effects (Table 1) of midsummer food and temperature conditions, had they been present, would have been reflected in the results obtained in the in situ life table experiments. In addition, physical limnological parameters of Wintergreen Lake (e.g., diel pH, weekly pH, dissolved oxygen) failed to show any marked deviations during the decline of the two Daphnia populations.

However, potential sources of mortality excluded from the in situ life table experiments do include predation by the bluegill (Lepomis macrochirus), Chaoborus punctipennis (Diptera) and Tropocyclops prasinus. Chaoborus punctipennis did not show any increase during the Daphnia declines, as has been commonly observed for cladoceran predators of Daphnia (Hall 1964, Wright 1965, DeBernardi 1974). The stable numbers of Chaoborus (5.32 ± 0.84/liter) in June and July presumably arose from a balance of natural population growth and predation by yellow perch (Perca flavescens); collections of adult yellow perch (> 150 mm std. length) in July showed that their limnetic feeding activity was almost entirely

confined to Chaoborus. The increased water temperature in midsummer may nevertheless result in increased predation rates by these potential daphnid predators (Fedorenko Their small head size (< 1.2 mm) makes it unlikely 1975). that any adult daphnids will be eaten (Swift and Fedorenko 1975), and any population-wide predation impact must be exerted through the juvenile size classes of the two populations (DeBernardi 1974, Hall et al. 1976). The small size of Tropocyclops prasinus (< 0.9 mm) makes it even less likely that mortality of adult Daphnia will result from their presence. That invertebrate predation is not the predominant mechanism involved in the disappearance of the two Daphnia species is supported by the persistence of juvenile size classes of the smaller and presumably more vulnerable species (D. galeata mendotae) during the disappearance of the adults of both populations.

Bluegill sunfish collected in mid-July were found to be eating all adult size classes of both <u>Daphnia</u> species. In addition, collections of sedimented seston during July showed that few undigested <u>Daphnia</u> reached the lake bottom compared to the thousands of <u>Daphnia</u> (> 90% of the total) found in fish fecal material. To the extent that these proportions reflect mortality of various kinds they further suggest the importance of planktivory relative to food, temperature, and physical factors in the decline of the two Daphnia populations.

The presumed importance of size-selective predation by bluegills in the observed declines of the two species of Daphnia can be tested further by examination of the age distribution of parthenogenic eggs carried by the females of each population. Edmondson (1968, 1974) discussed general considerations involved with departures from an even egg age distribution generated by a constant and continuous rate of egg laying without attendant population growth. Conditions favorable to population growth will result in an egg age distribution dominated by young eggs; the production of new eggs will parallel the increase in reproductive females occurring during population growth and young eggs will always outnumber older eggs. For a declining population, however, two extreme outcomes of egg age distribution analysis are possible. Populations which decline from a reduction in the rate of egg laying per female (with a constant mortality schedule as in the zero population growth situation) will be dominated by eggs in later stages of development. Conversely, a population which declines as a result of increased predation rate on egg-bearing individuals will show a preponderance of young eggs, since the probability that ovigerous females survive until their eggs hatch will decrease. Population declines resulting from interactions of increased predation and lowered egg laying rates will exhibit egg age distributions intermediate between these two extremes.

Egg age distribution analyses were performed for both <u>Daphnia</u> populations during the months of June and July following the resumption of parthenogenesis by <u>D. pulicaria</u>. The relative age of the eggs was determined by criteria stated in Table 2. Deviations from an even egg age distribution were quantified as the maximum deviation (d_{max}) of the observed cumulative egg age distribution from an even egg age distribution for each sampling date and time, as in the Kolmogorov-Smirnov test (Sokal and Rohlf 1969). Positive deviations were used to indicate dominance by young eggs, while negative values indicate a preponderance of older eggs. The range of values possible using the criteria in Table 2 is from +0.697 (only stage 1 eggs present) to -0.84 (only stage 5 eggs present).

Deviation values for <u>D</u>. <u>pulicaria</u> showed a steady increase from late June until the population disappeared in late July, consistent with the predation model and opposite to that expected from a population declining simply from constant mortality rates coupled with reduced rates of reproduction (Figure 13). This increase in d_{max} suggests that although <u>D</u>. <u>pulicaria</u> reproduction was reduced during this period, predation-related mortality was of overwhelming importance in determining the egg age distribution.

Figure 13. Distribution of d_{max} for <u>Daphnia</u> <u>pulicaria</u> (----) and <u>Daphnia</u> <u>galeata</u> <u>mendotae</u> (---) from midafternoon (o) and midnight (•) vertical tow samples.

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Deviation values for D. galeata mendotae corresponded to expectations for periods of population growth and decline due to predation (Figure 13). Population size increased until about June 17, when the population size temporarily stabilized and then began to decline (Figure 2). Declining d_{max} values prior to June 17 were expected from growing populations approaching their maximum densities; this trend was reversed as the population of D. galeata mendotae began to decline. If this decline had been due to a slowdown in reproduction, d_{max} values should have decreased further (and become negative) but instead they increased again, consistent with the effects of increasing predation. Just before their disappearance, mortality was sufficiently intense that only females bearing eggs in the first two stages of development (Table 2) were found in the population.

Although the data are not extensive, diel changes in d_{max} values are consistent with the interpretation given here (Figure 13). Limnetic activity by bluegills is generally restricted to daytime periods (Baumann and Kitchell 1974), so a lowering of the deviation of the egg age distribution from an even egg age distribution should be expected after nightfall. At this time, females with eggs in early stages of development will develop into later stages, and give rise to a more even egg age distribution. Synchrony in the timing of egg laying may

give rise to the diel changes in egg age distribution observed here, favoring newly laid eggs (positive d_{max}) after a short period of egg laying, and older stages (negative d_{max}) at some later time. However, it is unlikely that simple diel periodicity in egg laying could give rise to the more complicated patterns which developed among samples collected at the same time of day during the decline of Daphnia in Wintergreen Lake.

SPECIES SUCCESSION

The succession of <u>Daphnia pulicaria</u> by <u>D</u>. <u>galeata</u> <u>mendotae</u> in Wintergreen Lake appears typical of species succession of zooplankton congeners throughout the world (Hutchinson 1967). Only in the near-coincidence of the decline of both species' populations does the sequence in Wintergreen Lake appear unique; usually periods of decline of zooplankton congeners are separated by several weeks or months. The closeness of the population declines to the reproductive slowdown of <u>Daphnia pulicaria</u> also bears further investigation.

As was pointed out before, life table information showed that <u>D</u>. <u>galeata mendotae</u> was capable of continued reproduction throughout July, and that little variation in its capacity to increase (as measured by cohort r) occurred during the period of population decline (Figure 10). Another indication of continuing reproductive potential is the consistency of the brood sizebody size relationship in field samples collected during July (Figure 12). In contrast, little is known of seasonal variation in predation pressure on this species,

although analyses of population size structure and egg age distribution suggest it to be very important. If predation was severe enough in late July to cause such a precipitous and total disappearance of this species, why was it capable of an equally dramatic increase in June and early July?

One possible answer is that fish abundance and feeding activity in the limnetic zone increased in late July, resulting in increased mortality of <u>D</u>. <u>galeata mendotae</u>. Suggestive evidence that this may be true in Wintergreen Lake was obtained from trial runs of the sediment collecting jars (see p. 10) on May 4 and June 8, 1976. On neither of these dates did the sediment traps (n = 8) contain fish fecal material containing <u>Daphnia</u> as was observed during mid-July, although <u>Daphnia</u> molts and recently dead <u>Daphnia</u> were found in the traps.

A seasonal shift to limnetic feeding by bluegills which would result in these sediment trap results may be brought about by declining populations of littoral zone prey. Densities of <u>Simocephalus serrulatus</u> among the lily pads (<u>Nuphar</u>, <u>Nymphaea</u>) (Figure 1) declined noticeably from June to July, and bluegills collected in mid-June were found to be eating these littoral zone prey. Werner and Hall (pers. comm.) have observed a similar seasonal shift by bluegills to limnetic prey as littoral zone prey declined in abundance. Baumann and Kitchell

(1974) propose that diel migrations of bluegill between limnetic and littoral zones are related to the quantities of prey available in these areas.

In addition, the rapid reduction of population densities of D. pulicaria in mid-July may cause bluegills already normally residing in the limnetic zone to include greater numbers of D. galeata mendotae in their diets. In the period prior to its reproductive depression, D. pulicaria was just able to maintain its population density, even though its egg ratio showed that it was capable of increasing in numbers. This lack of population increase suggests that a balance was present between predation on this species and its predator-free rate of increase. As this species declined (following its reproductive collapse) planktivores present may have included (due to optimal foraging considerations: see Werner and Hall 1974) more of the smaller bodied but abundant D. galeata mendotae in their diets. That D. galeata mendotae suffered an increasing mortality during this period is born out by the reduction in large size classes present and by the increasing tendency for only females carrying younger, less advanced eggs to be represented in the population. Several other observations of a decline of D. pulicaria before that of D. galeata mendotae (Birge 1896, Hall 1964, 1971, Noble 1975) are consistent with this view. Additional analyses of prey species selection by

planktivores on a seasonal basis would aid in evaluating the possibility suggested here that declines in single species populations may lead to predation-related declines in other species.

EVOLUTION OF <u>DAPHNIA</u> LIFE HISTORY CHARACTERISTICS

The preceding discussion of the midsummer dynamics of two <u>Daphnia</u> species in Wintergreen Lake suggests certain similarities and differences in the reasons for the decline of these populations. To the extent that these results identify factors potentially important in the regulation of these two species in north temperate zone lakes, they also provide a basis for discussion of the evolutionary response of these species to typical midsummer conditions.

Certain features of the Wintergreen Lake system, such as size-selective predation by planktivorous fish and the tendency of <u>D</u>. <u>pulicaria</u> to avoid the epilimnion in midsummer, are also found in other lakes where these species occur. Similarly, the combination of bluegreen algae and high water temperatures associated with the abortion of parthenogenic eggs of <u>D</u>. <u>pulicaria</u> in Wintergreen Lake is common to many eutrophic lakes where this species occurs, and should be expected to play an important role in its evolution.

Daphnia pulicaria

Assessment of the effects of midsummer conditions on D. pulicaria is hampered by potentially erroneous designations of several populations of similar appearing species. Brooks (1957) considered D. pulicaria Forbes to be synonymous with D. pulex Leydig, and only recently have zooplankton workers in North America (Brandlova et al. 1972, Wong and Ward 1972, Ward and Robinson 1974) begun to routinely distinguish between these two species, as has been done much earlier in Europe (Hrbáček 1959, Hrbáčková-Esslová 1966). As a result, little ecological data exist for clearly defined populations of D. pulicaria. Hrbácek (D. J. Hall, pers. comm.) indicated that a Daphnia population from Oneida Lake, New York, previously identified as D. pulex (Hall 1971, Clark 1975, Noble 1975) is actually D. pulicaria. Dodson's current studies (pers. comm.) of Daphnia systematics suggest that Birge's (1895, 1896) Lake Mendota population of D. pulicaria reassigned since that time to D. schødleri (Brooks 1957, Hutchinson 1967) is probably also referable to D. pulicaria. In addition, my own collections of Daphnia from lakes studied by Haney and Hall (1975) show that the D. pulex populations reported by them are probably D. pulicaria instead (Table 3). Brandlova et al. (1972) indicated substantial physiological differences between D. pulex and D. pulicaria and concluded that the distribution of

these two species was pond and limnetic, respectively. In that numerous studies of <u>D</u>. <u>pulex</u> (<u>sic</u>) are based on collections from limnetic regions (e.g., Burns 1969, Arnold 1971, Crowley 1973) the amount of ecological information on <u>D</u>. <u>pulicaria</u> in North America may be greater than at first supposed. In the following discussion, information obtained from limnetic populations identified as either <u>D</u>. <u>pulex</u> or <u>D</u>. <u>pulicaria</u> will be used.

Limnetic populations of this species complex (D. pulex or D. pulicaria) are generally confined to colder waters, either being found in spring and autumn pulses (Hall 1964, Fott 1975, Noble 1975), or confined to hypolimnetic regions in midsummer (Table 3, Birge 1895, 1896, Hall 1964, Haney and Hall 1975). Management of highly eutrophic lakes by total aeration (Shapiro and Pfannkuch 1973) or hypolimnion aeration (Fast 1971) consistently results in either a numerical increase in this species or expansion of its vertical distribution to include the oxygenated, cool-water habitats.

Several components of the population growth (see review by Hall et al. 1976) of <u>D</u>. <u>pulicaria</u> have been shown to be negatively affected by typical midsummer resource, predator or temperature conditions, which may result in these distribution patterns and response to aeration. For example, the depressive effects of high temperatures (> 20°C) and large-celled bluegreen algae
on filtering and assimilation rates have been documented (Burns 1969, Arnold 1971, Crowley 1973); in addition, Arnold has shown that these effects are manifest in reduced reproduction and survivorship. Hrbáčková-Esslová (1962) and Brandlova et al. (1972) have reported that <u>D. pulicaria</u> is less efficient reproductively at 28°C than at either 20° or 24°C; Hrbáčková-Esslová also reported that eggs produced at 28°C often remained undeveloped.

The present study showed that food-temperature conditions present in the epilimnion and metalimnion in mid-July in Wintergreen Lake resulted in reduced rates of egg production and increased abortion of these eggs. These events occurred in 0.5 m, 2.5 m, 3.0 m, and 3.5 m incubations, but not in 4.5 m incubations where 0.5 m water and food had been cooled to temperatures at 4.5 m. This pattern suggests that temperature was of major importance but temperatures earlier and later in the summer were equal to those of mid-July (23-27°C); only the food conditions differed between this period and those of later and earlier. The size structure of the algal community shifts during mid-July from numerous small algae (e.g., Dysmorphococcus, Cyclotella, Cryptomonas) to fewer large-celled algae (e.g., Anabaena, Ceratium, Volvox). In late July increasing numbers of bacteria-detritus aggregates re-establish the high

densities of small (2.4-7.6µm diameter) particles. These shifts are apparent from photographs of settled water samples (Figure 14) and from size frequency distributions obtained by Coulter Counter analysis of samples from this period (Figure 15). Thus it appears that an interaction of food and temperature conditions brought about the reduction in egg laying and abortion of eggs observed in mid-July.

Lampert (1977) recently demonstrated that algae of large cell size were required in greater abundance to offset reduced filtering efficiency by <u>Daphnia pulex</u>. However, at lower temperatures the balance between assimilation and respiration could be achieved at lower concentrations of a given algal species. In this respect, the results obtained in Wintergreen Lake provide a natural example of the interaction of food and temperature effects observed by Lampert under laboratory conditions.

In spite of <u>D</u>. <u>pulicaria</u>'s ability to survive midsummer epilimnetic temperature and food conditions, they consistently avoided this habitat in Wintergreen Lake and in a number of nearby lakes (Table 3). The seasonal change in daytime vertical distribution of this population in Wintergreen Lake may be explained as a response to avoid visual predators which become more active in the limnetic zone during summer (Baumann and Kitchell 1974). However, the summer nighttime

Figure 14. Photographs of replicate fields (0.107 mm²; 5.28 μ 1) of settled water samples of algae collected from 0.5 m during July, 1976.



Figure 15. Abundance of algal particles of three size fractions and three dominant genera collected from 0.5 m during July, 1976. Note that <u>Anabaena and Ceratium</u> densities have been multiplied by 1000 for inclusion on these axes.





distribution of the species (concentrated in the metalimnion in Wintergreen Lake and in the hypolimnion when oxygen conditions permit) does not appear to be a strategy which results in maximization of population growth rate r as measured in the life table experiments. Only during a very short period in mid-July is cohort r higher in the hypolimnion incubations than in the epilimnion incubations (Figure 6). Approximately 60% of the three-fold variation in cohort r of D. pulicaria in the epilimnion incubations can be accounted for by variation in food particle density (2.39-7.6 µm diameter) on the cohort starting date. In the hypolimnion incubations (where epilimnion water was also used) only 3.4% of cohort r variation was attributable to food particle density. In view of the great sensitivity of D. pulicaria to changes in food conditions at epilimnion temperatures, the best strategy for this species for sustaining high population growth may be to avoid water depths where high temperatures occur. This is in spite of the ability of D. pulicaria to achieve positive population growth in epilimnion incubations throughout the summer.

Alternately, any temporary gain in population growth by <u>D</u>. <u>pulicaria</u> due to migration to warmer, epilimnion waters at night during good food periods may be offset by higher predation rates in these epilimnion waters. For example, bluegills may be sufficiently

effective in nocturnal feeding (cf. Keast 1970, Seaburg and Moyle 1964, Baumann and Kitchell 1974) that higher population growth rates are achieved by <u>D</u>. <u>pulicaria</u> by remaining in the hypolimnion or metalimnion. However, it is unclear if nocturnal feeding by bluegills occurred in this study, as collections made at dawn indicated a predominance of littoral zone feeding by these fish.

The hypothesis that predation by vertically migrating <u>Chaoborus</u> may influence the vertical distribution of <u>D</u>. <u>pulicaria</u> is untested due to the avoidance by <u>Chaoborus</u> of the Van Dorn samplers used in this study. However, the diel vertical migrations of <u>D</u>. <u>galeata men-</u> <u>dotae</u> suggest that diel variations in the depth distribution of <u>Chaoborus</u> are probably unimportant to the vertical migration of <u>D</u>. pulicaria.

Another possible explanation for <u>D</u>. <u>pulicaria</u>'s nighttime distribution involves the presence of <u>D</u>. <u>galeata</u> <u>mendotae</u>. Although <u>D</u>. <u>pulicaria</u> survives in water from which <u>D</u>. <u>galeata mendotae</u> has been removed by filtration (see methods and materials section, In situ life table experiments), the possibility of either aggressive interaction or the secretion of allelochemic substances by <u>D</u>. <u>galeata mendotae</u> exists. Responses by zooplankton to physical disturbance by other zooplankton (Strickler and Bal 1973, Fryer 1957) or the secretion of water-borne organic compounds (Banta 1939, Banta and Brown 1929,

Dahl et al. 1970, Katona 1973, Griffiths and Frost 1976) are well documented. Strickler (pers. comm.) has observed that as part of the avoidance reaction of zooplankton prey to predators, feeding activity is reduced while swimming speed is increased. The effect of similar encounters among potential competitors on food intake and population growth has not yet been determined. However, the lack of a density effect on cohort r in this study makes it unlikely that physical disturbance of <u>D. pulicaria</u> by <u>D. galeata mendotae</u> is of major importance in the diel vertical distribution of D. pulicaria.

Any chemical compounds released by <u>D</u>. <u>galeata mendotae</u> responsible for the restriction of <u>D</u>. <u>pulicaria</u> to the metalimnion must be volatile or rapidly broken down, or their presence in freshly collected water would have influenced the animals in the life table experiments. As the water was aired slightly (to remove zooplankton) any volatiles may have been lost. If the product is only produced at night when <u>D</u>. <u>galeata mendotae</u> is found in the epilimnion and rapidly broken down during the day (by sunlight, for example) it would not have been included in water collected in mid-afternoon and used in the in situ life table incubations of <u>D</u>. <u>pulicaria</u>. The role of allelochemic compounds in zooplankton succession obviously requires further study.

Daphnia galeata mendotae

In contrast to D. pulicaria, D. galeata mendotae is generally thought of as a warm-water species by virtue of its midsummer epilimnetic distribution (Hall 1964, Tappa 1965, Haney and Hall 1975, Table 3) and its capacity for active reproduction in midsummer (Hall 1964, 1971, Tappa 1965, Cummins et al. 1969). In the present study, D. galeata mendotae failed to show any mid-July reproductive decline in epilimnion incubations. Burns (1969) found no depressive effect of high temperature on filtering rate as she had for D. pulex. D. galeata mendotae appears to be far more susceptible to predation than to food or temperature conditions, as indicated by Hall (1964, 1971), Suffern (1973) and in the present study. Whether or not its large-headed, summer morphs are less vulnerable to predation by invertebrates than noncyclomorphic forms is as yet untested.

Discussion

Differences between <u>Daphnia pulicaria</u> and <u>D</u>. <u>galeata mendotae</u> include preferred habitat, reproductive response to midsummer algae-temperature conditions and laboratory-measured filtering rates at various temperatures. Probably most significant, however, are differences in the body size of these two species and their tendency to produce resting eggs or epphipia. Whether or not these differences are due to past evolutionary

pressures similar to those which resulted in the midsummer declines of these two species in Wintergreen Lake is, of course, unknown. However, a possible test of the generality of the results obtained in this study would be to examine current life history characteristics of these two species for consistency with the interpretations given earlier on the importance of various factors in bringing about the midsummer decline.

As indicated in Table 4, D. pulicaria tends to produce a larger egg, mature at a larger size and ultimately reach a larger body size than does D. galeata mendotae. This undoubtedly makes D. pulicaria more vulnerable to size-selective predators such as the bluegills found in Wintergreen Lake. The tendency for these two species to produce enlarged helmets in midsummer (cyclomorphosis) is also consistent with their vulnerability to sizeselective predators. D. galeata mendotae, by reducing its body length and producing a large helmet instead, may increase its reproductive rate (Brooks 1966), while decreasing its vulnerability to both vertebrate and invertebrate predators (Brooks 1966, Dodson 1974). D. pulicaria, which is larger in size than D. galeata mendotae, does not produce enlarged helmets, presumably because the resulting reduction in body size or visibility due to use of this tactic is insufficient to substantially reduce mortality from size-selective predators. Instead,

Characteristic	<u>D. pulicaria</u>	D. galeata mendotae
Filtering rate temperature optimum	20°C	25°C
Preferred midsummer habitat	Metalimnion, hypolimnion	Epilimnion, metalimnion
Diel vertical migration	Restricted to water cooler than 22°C	Pronounced, to epilimnion
Response to bluegreen algae, high temperature conditions	Reduced reproduction, egg abortion	No adverse effect
Seasons of epphipia production	Spring, autumn	Autumn
Egg size (Stage 1, max. dimension)	0.27 mm	0.19 mm
Size at first reproduction	1.0-1.2 mm	0.8-1.0 mm
Adult body size	1.0-2.4 mm	0.8-2.0 mm
Slope of brood size-body size relationship	Gentle	Steep
Cohort r versus temperature	Identical relationship for	both species

Table 4. Summary of life history characteristics of <u>Daphnia</u> <u>pulicaria</u> and <u>Daphnia</u> <u>galeata</u> <u>mendotae</u>.

<u>D. pulicaria</u> appears to devote its energies to increase carapace length (exclusive of helmet) and, indirectly, also increase brocd size. The tradeoffs involved with these strategies are discussed more fully in Hall et al. (1976).

The other major difference between these two species is their propensity to produce resting eggs or D. pulicaria produces resting eggs in spring epphipia. and autumn (Stross 1973, this study), whereas D. galeata mendotae produces these resting eggs in autumn (Haney and Hall, 1975, Hall, pers. comm., this study). It appears that the tendency to produce resting eggs in spring is a characteristic associated with the species more likely to be eliminated in midsummer. Conditions which cause D. galeata mendotae to disappear in midsummer (as in Wintergreen Lake) may be sufficiently rare as to not have resulted in the evolution of an early-summer, epphipia-producing phenotype of this species. In lakes where D. galeata mendotae does not go extinct in midsummer, there is a reproductive advantage to producing parthenogenically until autumn. Only two resting eggs per every other instar are produced via epphipial reproduction, while the cumulative effect of parthenogenic population growth over an entire summer at a rate of 2-15 eggs per adult instar would probably overwhelm the net contribution of early-epphipia strategists. Only in

the case of a large-bodied species such as <u>D</u>. <u>pulicaria</u> likely to be eliminated during midsummer would it be profitable in spring and early summer to produce epphipia at the expense of more numerous parthenogenic offspring.

Alternately, production of epphipia by <u>D</u>. <u>pulicaria</u> may be in response to temporary conditions not encountered during June and July when both species were present. During early May, chlorophyll a (corrected for phaeopigments) was undetectable and particulate carbon was at its springsummer low of \approx 1 mg/liter (Klug et al. unpubl. data). Thus, production of epphipia may have been the only kind of reproduction resulting in viable offspring at that time. Since life tables were not run for either species during this period, it is difficult to assess whether continued parthenogenic reproduction would have resulted in population growth.

Thus, care must be taken to avoid acceptance of all life history characteristics only as adaptations to intense predation without consideration of alternate hypotheses. A great deal has been written about sizerelated aspects of competitive abilities in zooplankton, and it is interesting to consider the life history characteristics of these two species (Table 4) in light of competitive effects not observed in this study. For example, during the decline of these two species all size classes of D. galeata mendotae carried more eggs than

corresponding size classes of D. pulicaria. In response to this apparent competitive superiority of D. galeata mendotae it might be supposed that D. pulicaria evolved to be a larger animal, sacrificing high egg production for an increased ability to withstand periods of food shortage (Threlkeld 1976) or ingest a wider size spectrum of food particles (Burns 1968, Hall et al. 1976). Examination of the life table data collected in this study shows that this interpretation is only partially satisfactory. Although it does appear that D. galeata mendotae is more efficient than D. pulicaria in egg production, this is not reflected in higher population growth rates; the relationships between cohort r and temperature for both species are indistinguishable (Figure 16). Thus, for resource and temperature conditions as experienced by these two species in Wintergreen Lake, their population growth rates are identical. Only in the face of predation do their strategies result in different population growth rates. Potential differences in competitive abilities of these two species may appear at different seasons or under different resource conditions, but were not observed in this study. In contrast, all aspects of the life history characteristics of these two species appear consistent with a dominant influence of planktivory in their evolution and seasonal association in Wintergreen Lake.

Figure 16. The relationship between cohort r and temperature of <u>Daphnia pulicaria</u> (•) and <u>D. galeata mendotae</u> (o) as determined in in situ life table experiments at all incubation depths.

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Figure 16

SUMMARY AND CONCLUSIONS

Of the four major factors associated with the midsummer decline of Daphnia populations, only one, predation by vertebrate predators, is consistent with the results obtained in this study. Midsummer food and temperature conditions, although having a dramatic influence on reproduction, were not sufficient to bring about the elimination of either species of Daphnia, even in the epilimnion which D. pulicaria appears to naturally avoid. The importance of predation by bluegills in the midsummer decline of Daphnia in Wintergreen Lake was indicated by gut analyses of these predators, collection and identification of remains of fecal material which settled to the lake bottom, shifts in the size structure of the Daphnia populations during their declines, and changes in the age distribution of parthenogenic eggs being carried by the females of the populations.

In addition, the apparent life history characteristics of the two populations of <u>Daphnia</u> in Wintergreen Lake appear consistent with planktivory as a major selective pressure in their evolution. It remains to

be seen if the life history tactics of other daphnid species living under different predatory regimes differ significantly from the life history features observed here.

Although the major focus of this research was on a population and evolutionary level, the study also points out the need for further research into the physiological responses of daphnids to midsummer food and temperature conditions. This need is especially acute where several factors interact, as observed in the reduction of egg production and abortion of parthenogenic eggs.

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