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Competition, predation and the relative abundances of two species of *Daphnia*

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Abstract. We investigated the factors controlling the relative abundances of two *Daphnia* species, *D. pulex* and *D. laevis*, in a small Wisconsin pond. *D. pulex* was the dominant *Daphnia* species in fall 1977 and summer-fall 1978; *D. laevis* was the only *Daphnia* species present in summer 1979. The abundance of *D. laevis* was positively correlated with the abundance of the notonectid, *Buenoa confusa*. In predation trials, notonectides exhibited a distinct preference for *D. pulex* over similarly-sized *D. laevis*, but *Chaoborus* larvae fed at similar rates on both *Daphnia* species. Behavioral observations revealed that *Buenoa* adults were much less efficient at capturing *D. laevis* than *D. pulex*. Quantitative results of these predation trials were combined with estimates of predator and prey density and distribution to evaluate the effect of predation on the daphnid populations. The effect of predation varied through time and microhabitat, and only infrequently could predation account for total prey mortality. *D. laevis* was most abundant at times and in places where *Buenoa* predation was most intense. Competition experiments illustrated the competitive superiority of *D. pulex* over *D. laevis*. *D. pulex* was able to competitively exclude *D. laevis* in long term experiments, and *D. pulex*'s fecundity was higher than that of *D. laevis* in shorter experiments. In long-term experiments, *Chaoborus* larvae at natural densities were able to keep both *Daphnia* species at low, constant levels and neither species clearly dominated when *Chaoborus* was present. The relative abundances of *D. pulex* and *D. laevis* were controlled by a complex of biotic and abiotic factors. Pond depth and predator density determined the intensity of predation on daphnid populations. When notonectid predation was intense, *D. laevis* dominated; when the intensity of predation by notonectids was low, *D. pulex* dominated due to its superior competitive abilities. At different times selective predation or high resource levels promoted the co-existence of these two species.

Introduction

A number of recent studies have examined the roles of competition and predation in determining the distributions and abundances of aquatic organisms (reviewed in Connell, 1975 and Zaret, 1980). Many of these studies have shown that selective predation on competitively-superior prey species allows the co-existence or numerical dominance of competitively-inferior species (Paine, 1966; Neill, 1975; O'Brien and Vinyard, 1978; Jacobs, 1977, 1978; Zaret, 1972a, 1972b). These competitively-inferior species often possess a variety of morphological and behavioral adaptations which reduce the impact of predators on their populations. The energetic costs or reproductive constraints associated with these antipredator adaptations, however, may limit the competitive success of these species in predator-free environments (O'Brien and Vinyard, 1978; Kerfoot, 1975, 1977b; Jacobs, 1978). While abiotic factors and food abundance are important in some instances (Neill, 1978; Burns, 1969), many studies suggest that the intensity of selective predation determines the relative abundances of prey species

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(Zaret, 1980).

Two *Daphnia* species, *D. laevis* and *D. pulex*, showed large year-to-year variations in relative abundance in a small Wisconsin pond. The relative abundance of *D. laevis*, which possesses a longer helmet and tail spine than *D. pulex*, was positively correlated with the densities of the notonectid *Buenoa confusa*. Behavioral observations and data from field populations led us to hypothesize that selective predation by *Buenoa* determines the relative abundances of these two *Daphnia* species. In the following study, field observations and laboratory experiments were used to test this hypothesis.

Study site

Bavarian Sausage Pond is a semi-permanent pond occupying a closed basin 9 km southwest of the University of Wisconsin-Madison campus on U.S. Highway 18/151 (Figure 1). In early September, 1977, the pond's maximum depth was 36 cm. Water levels declined through the fall of 1977, and the pond dried completely by November 22. The pond refilled with snow-melt water in the spring of 1978, but had dried by mid-June. Heavy rains in mid-June, 1978, filled the pond to a maximum depth of 1.5 m and a maximum surface area of 1.6 ha. Water levels declined thereafter, reaching a least maximum depth of 45 cm by September 8, 1978. Maximum water depths in the fall of 1978 and the summer of 1979 were <40 cm. Although there was some day-to-day variation, mid-afternoon surface water temperatures in the summers of 1978 and 1979 usually remained between 20 and 24°C. In general, surface water temperatures began to decline by mid-September reaching 10°C by early October and 5°C by November. Unseasonably warm weather, however, resulted in surface water temperatures of 19°C as late as 18 September in 1978. Dense vegetation (*Polygonum* sp. in 1977, *Scirpus fluviatilis* in 1978 and 1979) covered large portions of the basin in all years.

Methods and Results

Field sampling

We estimated the relative abundances of zooplankton species by towing a 93 μ mesh, 0.3 m plankton net while wading across the pond at 1–4 week intervals in the fall of 1977, summer and fall of 1978, and the early summer of 1979. B. Schnagl kindly provided us with information on the relative abundances of *Daphnia* spp. and their predators from late July to September 1979; however, relative abundances of other cladocerans were only determined in early July in 1979. We took quantitative zooplankton samples with a 2 l Van Dorn bottle at weekly to biweekly intervals from July 7 to September 1, 1978, from 8 stations. Single samples were taken from each shallow-water station (<30 cm deep, Stations 1, 6, 7, and 8), and three samples, representing surface, mid-depth, and bottom water strata, were taken from each deep-water station (>30 cm deep). We took nine samples (three in each stratum) from deep-water Station 2 on September 21. The deep-water stations were further classified as open water (Stations 2 and 5), vegetation (Station 4), and vegetation-open water interface (Sta-

tion 3) stations (Figure 1). We took five quantitative zooplankton samples in the pond on July 12, 1979 with an 865 ml jar. We concentrated samples through 52 μ mesh, decanted the filtrate into 130 ml jars, and preserved filtered zooplankton with 95% ethanol. All life history stages of zooplankton in the quantitative samples and aliquots from qualitative samples were identified and counted at 12–25 x under a dissecting microscope. We measured helmet heights, core body lengths, and tail spine lengths of *Daphnia* spp. by placing specimens on an inverted microscope and measuring projected silhouettes with a Hewlett-Packard 9100 B digitizer (Figure 2). If numbers were very high (>100 individuals), we measured subsamples of 20–60 individuals of each species on each sampling date; otherwise all individuals were measured. We used data on population, egg, and embryo densities for each cladoceran species to calculate the instantaneous rate of change, r , instantaneous birth rate, b , and the instantaneous death rate, d , by Edmondson's egg ratio method (Edmondson, 1960) with Paloheimo's correction (1974) for the instantaneous birth rate and with correction for changes in pond volume (Cooper, 1979).

We took qualitative macroinvertebrate samples with a dip net in fall 1977 and 1978, and summer 1978 and 1979. We took quantitative macroinvertebrate samples with an open-ended aluminum box sampler, 38 cm x 38 cm x 130 cm high, at three random deep-water stations every 1–4 weeks in 1978 and on one date (July 12) in 1979. The box was plunged into the substrate and the enclosed

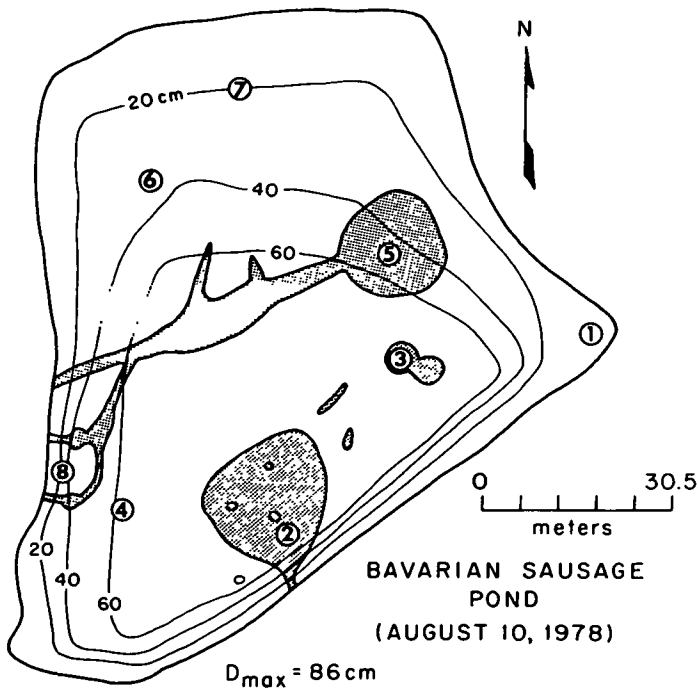


Fig. 1. Map of Bavarian Sausage Pond. Stippled areas represent open water areas, numbers in circles are sampling stations, and depth interval is 20 cm.

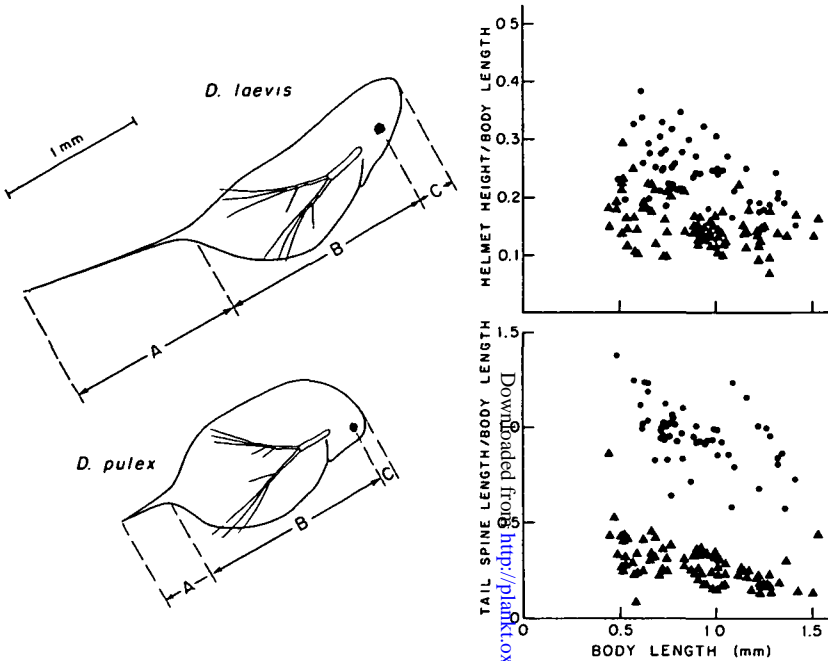


Fig. 2. *Daphnia laevis* and *Daphnia pulex*. A = helmet height, B = core body length, C = tail spine length, A + B = total body length. The graphs represent the relationships between helmet height to core body length ratios and core body lengths, and between tail spine length to core body length ratios and core body lengths for both species. Dots represent measurements for *D. laevis*, triangles represent measurements for *D. pulex*. When the two *Daphnia* species co-occurred in 1978 the total body lengths of *D. laevis* and *D. pulex* ranged from 0.62 to 1.66 mm and 0.52–2.41 mm, respectively. The smallest ovigerous *D. laevis* measured 1.51 mm (total body length) and the smallest ovigerous *D. pulex* measured 1.30 mm (total body length).

water column was repeatedly sampled with an aquatic insect net until 3 consecutive sweeps yielded no additional animals. We separated the macroinvertebrates from debris and vegetation in the field, preserved them in 70% ethanol, and subsequently identified and counted them at 6–12 x with a dissecting microscope. Head lengths of larvae of the dipteran *Chaoborus* and head widths of the other insect predators were measured at 12–25 x with an ocular micrometer. We collected *Chaoborus* larvae with both Van Dorn and macroinvertebrate samplers. The higher density estimate for a given *Chaoborus* instar produced by either of these sampling methods was used as the actual density estimate for that instar on that sampling date. In general, Van Dorn samples gave the higher density estimates for early instar *Chaoborus* larvae, while macroinvertebrate samples gave the higher density estimates for late instar *Chaoborus* larvae. We made direct observations of macroinvertebrate behavior and distribution while wading through the pond or from an observation platform placed in the pond.

In the fall of 1977 the pond was very shallow (<36 cm) and *Ceriodaphnia* spp. were the dominant cladocerans (Table I). Large *Anax junius* naiads and adult *Notonecta undulata* were abundant predators in early September but declined

Competition, predation and abundance of *Daphnia*

Table I. Species composition of cladoceran assemblage, dominant insect predators, and depth of Bavarian Sausage Pond, 1977–79.

	Fall 1977	Summer-Fall 1978	Summer 1979
Maximum depth	0–36 cm	45–120 cm	<31 cm
Dominant <i>Daphnia</i> sp. (% of total <i>Daphnia</i> numbers)	<i>D. pulex</i> (60–100)	<i>D. pulex</i> (92–100)	<i>D. laevis</i> (100)
Dominant cladoceran sp. (% of total cladoceran numbers)	Sept., Oct.: <i>Ceriodaphnia</i> spp., <i>C. affinis</i> and <i>C. laticaudata</i> (83–99) Nov.: <i>Daphnia pulex</i> (42)	Open water: <i>D. pulex</i> (37–90) Vegetation: <i>Simocephalus vetulus</i> (16–73) <i>Pleuroxus denticulatus</i> (3–72, most abundant in Aug.)	<i>D. laevis</i> (52)
Other common cladoceran spp. (% of total cladoceran numbers)	none	All habitats: <i>Moina affinis</i> (0–57, abundant only in early July) <i>Ceriodaphnia</i> spp. (1–41) Vegetation: <i>D. pulex</i> (2–45, most abundant in vegetation in July)	<i>Scapholeberis kingii</i> (33) <i>Simocephalus vetulus</i> (15)
Dominant predators	<i>Chaoborus americanus</i> larvae (particularly Oct.) <i>Notonecta undulata</i> adults (early Sept.) <i>Anax junius</i> naiads (early Sept.)	<i>Chaoborus</i> larvae <i>Anax</i> naiads <i>Notonecta</i> (all stages) <i>Buenoa margaritacea</i> (all stages)	<i>Chaoborus</i> larvae <i>Buenoa</i> (all stages) <i>Notonecta</i> (all stages)

rapidly to low levels by October. Larvae of *Chaoborus americanus* were common in later September and October. In 1978 the pond was much deeper (45–120 cm maximum depth), *D. pulex* was the dominant pelagic cladoceran, and *Chaoborus* larvae, *Anax* naiads, and the notonectids *Notonecta* and *Buenoa confusa* were the dominant predators (Table I, Figures 3 and 4). In the summer of 1979, the pond was very shallow (<31 cm), *D. laevis* was the dominant cladoceran species, and *Chaoborus* larvae and notonectids, particularly *Buenoa*, were the principal predators. The only other common cladocerans through 1978 and 1979 were littoral species (*Simocephalus*, *Pleuroxus*, or *Scapholeberis*, Table I).

The appearance of *D. laevis* in 1978 coincided with the appearance of *Buenoa* (Figures 4 and 5). In 1978, *D. laevis* was first collected in the vegetated and vegetation-open water interface habitats, and the relative abundance of *D. laevis* tended to be higher in the vegetated than in the non-vegetated habitats

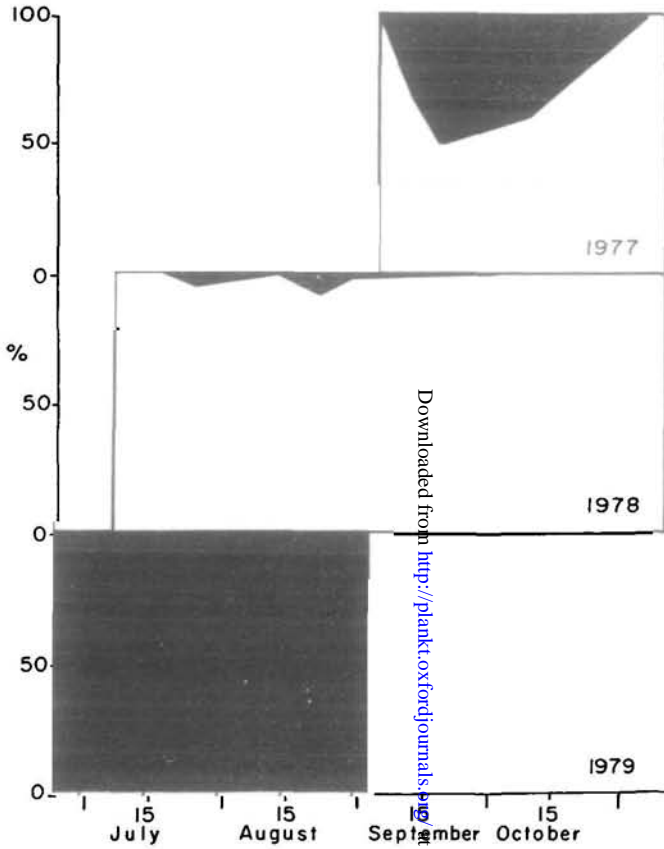


Fig. 3. Relative abundances of *D. laevis* (black) and *D. pulex* (white) in fall, 1977, summer, 1978, and summer, 1979.

(7.1–36.8% versus 0.3–1.8% of total *Daphnia* numbers, except for August 14 when *D. laevis* were virtually absent in all habitats). *D. pulex* densities and *D. laevis* densities were positively correlated ($r_s = +0.80$) in the open water habitat and negatively correlated ($r_s = -0.77$) in the interface and vegetated habitats ($p < 0.05$, Spearman rank correlation). *D. laevis* was never collected near the pond's edge (<30 cm) and *D. pulex* was rare there. *Anax* naiads and *Buena* were generally confined to vegetated areas, while most *Notonecta* adults were found in open-water areas, and *Chaoborus* larvae were distributed throughout the pond.

D. pulex was consistently more abundant in mid-depth strata than in surface strata in 1978 ($p < 0.05$, sign test), while *D. laevis* tended to be found in shallower strata. *Notonecta* typically rested at the pond's surface, while *Buena* was usually observed cruising at depths of 3–30 cm in small open areas within the dense *Scirpus* stands, approaching the surface only briefly to replenish its air supply. *Chaoborus* larvae were significantly more abundant in mid-depth and bottom water strata than in surface water strata ($p < 0.05$, sign test), and *Anax* naiads perched on vegetation or sat on the pond bottom.

Competition, predation and abundance of *Daphnia*

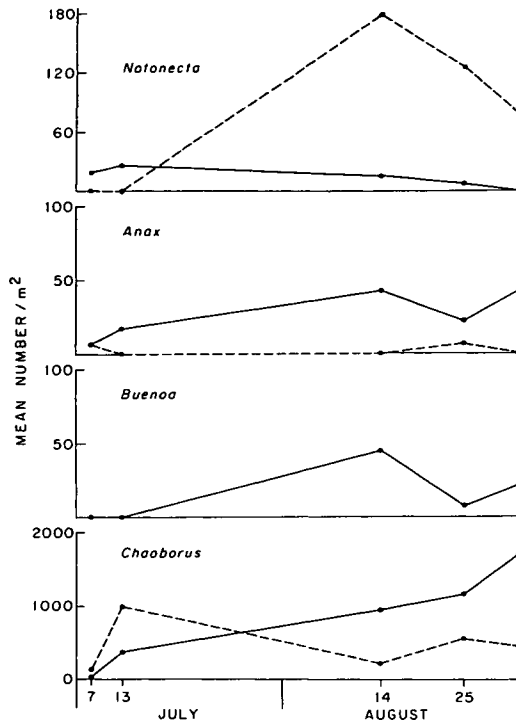


Fig. 4. Fluctuations in the density of the common insect predators in 1978. The solid line represents vegetated areas and the dashed line represents open water areas.

There were few trends or significant differences in growth rates, birth rates, and death rates among habitats or between *Daphnia* species, although *D. laevis* birth rates were significantly higher in the open water habitat than in the interface or vegetated habitats (Table II). Mean total lengths of *D. laevis* tended to be greater than mean total lengths of *D. pulex* in late July and August, but the only significant difference was recorded on July 27 ($p < 0.05$, Wilcoxon rank sum test).

Although qualitative samples indicated an abundance of *D. laevis* and *Buenoa* throughout the summer of 1979, quantitative samples were taken only on July 12. Average *D. laevis* density on this date was 22.6 l^{-1} , over five times higher than *D. laevis* densities collected at any station in 1978, and the instantaneous birth rate (b) was 0.45. Mean densities of *Buenoa*, *Notonecta*, and *Chaoborus* were 42 m^{-2} , 16 m^{-2} , and 5.2 l^{-1} at this time.

Predation trials: the impact of predation on Daphnia populations

In laboratory experiments, *Notonecta undulata* adults, large *Anax junius* naiads, and *Buenoa confusa* adults were simultaneously presented with equivalent initial densities of adult *D. pulex* and adult *D. laevis*. We presented late instar *Chaoborus* (IV) larvae with equivalent initial densities of similarly-sized (0.7 mm) juvenile *D. pulex* and *D. laevis*. We conducted the predation ex-

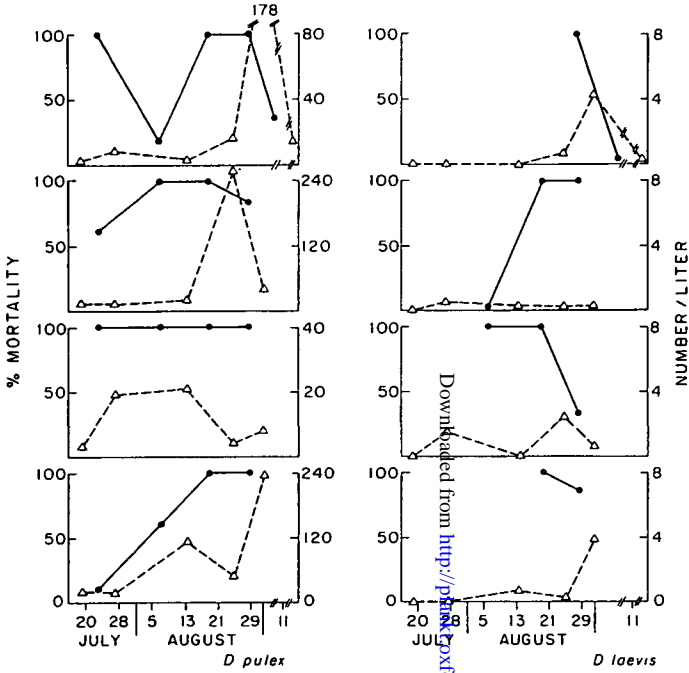


Fig. 5. Proportion (%) of total mortality attributable to predation (solid lines) for *Daphnia pulex* (graphs on left) and *D. laevis* (graphs on right), and population fluctuations of these two species (dashed lines) at all deep-water stations during the time they co-occurred in 1978. From top to bottom, these graphs represent Stations 2, 3, 4, and 5.

periments in glass containers 258–1740 ml in volume filled with filtered (52μ) pond water at 22°C under constant illumination from a fluorescent light source. Predators were either taken directly from the field or starved in the laboratory for less than one day prior to use in experiments. Control jars contained no predators. In most experiments the difference between initial and final prey numbers in the experimental jars was corrected for control mortality (Healy, 1952) and taken as an estimate of the number of prey eaten during the trial period. In some *Buenoa* trials, however, prey were replenished as they were eaten. Depending on the rate of prey disappearance, trial periods lasted from 0.5 to 24 h. From these data we calculated predator clearance rates (k) as in Dodson (1975). Clearance rates have the dimensions “liters cleared of prey per predator per day” and are constant and equivalent to the “attack rate” or “searching efficiency constant” if there is a linear relationship between number of prey consumed per predator and prey density (Hassell, 1978).

In addition, we conducted behavioral observations of predator-prey interactions under bright sunlight at 22°C in 1.75 l aquaria filled with filtered (52μ) pond water. We starved predators for one day prior to use in behavioral trials. Equal numbers of comparable-sized *D. pulex* and *D. laevis* (1.5–1.6 mm) were presented to each predator, and prey were replaced as they were eaten. Since nearly all predator-prey encounters resulted in predator attacks, we reported only

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Table II. Growth rates (*r*), birth rates (*b*), and death rates (*d*) for *Daphnia pulex* (P) and *D. laevis* (L) in 1978.

Interval		Station							
		Open water				Interface		Vegetation	
		2		5		3		4	
	P	L	P	L	P	L	P	L	
July 7–	<i>r</i>	0.00	–	+0.30	–	–0.48	–	–0.09	–
July 13	<i>b</i>	0.29	–	0.22	–	0.03	–	0.17	–
	<i>d</i>	0.29	–	–0.08	–	0.51	–	0.26	–
July 13–	<i>r</i>	–0.28	–	–0.38	–	+0.19	–	–0.27	–
July 19	<i>b</i>	0.53	–	0.11	–	0.26	–	0.32	–
	<i>d</i>	0.81	–	0.49	–	0.07	–	0.59	–
July 19–	<i>r</i>	+0.20	–	–0.03	–	0.00	–	+0.18	–
July 27	<i>b</i>	0.05	–	0.22	–	0.42	–	0.17	–
	<i>d</i>	–0.15	–	0.25	–	0.42	–	–0.01	–
July 27–	<i>r</i>	–0.07	–	+0.07	–	0.00	–0.05	–0.03	0.00
Aug. 14	<i>b</i>	0.27	–	0.30	–	0.14	0.00	0.00	0.00
	<i>d</i>	0.34	–	0.23	–	0.14	0.05	0.03	0.00
Aug. 14–	<i>r</i>	+0.13	–	–0.08	–0.03	+0.20	–0.06	–0.20	–
Aug. 25	<i>b</i>	0.00	–	0.00	0.00	0.08	0.00	0.05	–
	<i>d</i>	–0.13	–	0.08	–0.03	–0.12	0.06	0.25	–
Aug. 25–	<i>r</i>	+0.37	+0.28	+0.22	+0.46	–0.34	–0.02	+0.07	–0.24
Sept. 1	<i>b</i>	0.20	0.39	0.10	0.74	0.10	0.00	0.00	0.09
	<i>d</i>	–0.17	0.11	–0.12	0.28	0.44	0.02	–0.07	0.33
Sept. 1–	<i>r</i>	–0.10	–0.13	–	–	–	–	–	–
Sept. 21	<i>b</i>	0.16	0.12	–	–	–	–	–	–
	<i>d</i>	0.16	0.25	–	–	–	–	–	–

attack rates, capture rates, and ingestion rates here. We calculated capture success (the proportion of attacks resulting in successful capture) and ingestion efficiency (the proportion of captures resulting in successful ingestion) from these data.

We used clearance rate values reported here and in Cooper (1979) to construct a matrix of clearance rate values for different sizes of *D. pulex* and *D. laevis*, and different sizes of their predators. Clearance rates were assumed to remain relatively constant with changing prey density (Dodson, 1975; Cooper and Goldman, 1980). The assumptions of this model and its application to complex natural assemblages are examined in Cooper (1979). We used these predation rates and field information on the size structure, spatial distribution, and abundances of predators and prey to calculate a death rate due to predation (*d'*). We compared these death rates induced by predation to total cladoceran death rates (*d*) determined from field data to determine the proportion of observed prey mortality attributable to predation.

In the predation trials *Notonecta* adults consistently preferred *D. pulex* adults over *D. laevis* adults ($p < 0.05$, sign test, Table III). In trials using *Buena* as the predator, the mean clearance rate on *D. pulex* was over 8 times higher than the mean clearance rate on *D. laevis*. Medium-sized *Anax* naiads (head width =

Table III. Results of predation trials.

Predator	n	<i>D. pulex</i> <i>k</i> $\bar{X}(\pm s_x)$	<i>D. laevis</i> <i>k</i> $\bar{X}(\pm s_x)$
<i>Notonecta</i> adults	6	0.58(±0.14)	0.30(±0.12) ^a
<i>Buenoa</i> adults	6	21.37(±3.77)	2.60(±1.21) ^a
<i>Anax</i> naiads (head width = 4.4–4.7 mm)	3	1.70(±0.56)	2.16(±0.10)
<i>Anax</i> naiads (head width = 5.0–7.7 mm)	3	1.27(±0.54)	0.43(±0.25)
<i>Chaoborus</i> IV larvae	5	0.07(±0.03)	0.10(±0.02)

Notonecta adults, *Buenoa* adults, and *Anax* naiads were fed *Daphnia* spp. adults, and *Chaoborus* IV larvae were fed *Daphnia* spp. juveniles. n is the number of trial replicates and *k* is the clearance rate (number of liters cleared predator⁻¹ day⁻¹). Mean length of *D. pulex* adults = 1.60 mm, $s_x = 0.04$; *D. laevis* adult \bar{X} total length = 1.53 mm, $s_x = 0.03$; juvenile *D. pulex* \bar{X} total length = 0.71 mm, $s_x = 0.01$; and juvenile *D. laevis* \bar{X} total length = 0.71 mm, $s_x = 0.02$. ^aSignificantly different at *p* < 0.05 level (sign test).

Table IV. Behavioral observation on *Buenoa*-*Daphnia* spp. interactions. Each trial lasted from 0.6 to 1.7 h. P = *Daphnia pulex*, L = *Daphnia laevis*.

Individual predator	Attacks/h		Captures/h		Ingestions/h		Capture success (%)		Ingestion efficiency (%)	
	P	L	P	L	P	L	P	L	P	L
<i>Buenoa</i> 1	16.0	28.0	10.0	4.0	10.0	2.0	62.5	14.3	100.0	50.0
<i>Buenoa</i> 2	22.4	6.0	14.9	1.5	13.4	1.5	66.5	25.0	90.0	100.0
<i>Buenoa</i> 3	13.2	13.2	8.4	0.0	8.4	0.0	63.6	0.0	100.0	–
<i>Buenoa</i> 4	18.0	4.0	14.0	0.0	14.0	0.0	77.8	0.0	100.0	–
<i>Buenoa</i> 5	24.1	18.1	15.7	3.6	13.2	3.6	65.0	20.0	85.0	100.0
<i>Buenoa</i> \bar{X} (1–5)	18.7	13.9	12.6	1.8	11.8	1.0	67.1	11.9	95.0	83.3

4.4–4.7 mm) and *Chaoborus* IV larvae exhibited no consistent preferences for either *Daphnia* species, but large *Anax* naiads (head width = 5.0–7.7 mm) preferred adult *D. pulex* over similarly-sized *D. laevis* in all three trials.

In five behavioral trials, *Buenoa* adults consumed adult *D. pulex* 8.4 times faster than similarly-sized *D. laevis* (Table IV). This result was primarily the product of a higher *Buenoa* capture success for *D. pulex* than for *D. laevis*. On average, 67% of *Buenoa*'s attacks on adult *D. pulex* resulted in successful captures, while only 12% of *Buenoa*'s attacks on *D. laevis* resulted in successful captures. The results of the predation trials and behavioral observations indicate that notonectids, and perhaps large *Anax*, show significant preferences for *D. pulex* over similarly-sized *D. laevis*. At least for *Buenoa*, this prey preference is the result of differential capture efficiencies for each *Daphnia* species.

The proportion of prey mortality attributable to predation was calculated by using clearance rates from predation trials and field data on the sizes, abundances, and distributions of predators and prey. *Chaoborus* predation accounted for greater than 90% of the mortality due to predation for both *Daphnia* species in the non-vegetated habitats. Predation by *Notonecta* adults and *Anax* naiads

was of occasional minor importance. In the vegetated habitat, on the other hand, *Chaoborus* predation accounted for 71–84.4% of the predator-induced *D. pulex* mortality and variable proportions (20.2–97.8%) of the predator-induced *D. laevis* mortality. Odonate and notonectid predation accounted for the remainder of the predator-induced *D. pulex* mortality, and odonate predation accounted for most of the remainder of the predator-induced *D. laevis* mortality.

Total mortality induced by predators (d'), *Chaoborus* d' values, and, in the vegetation, non-chaoborid insect d' values were consistently higher for *D. pulex* than for *D. laevis*. This result could be attributed to three factors: (1) *D. laevis*'s tendency to occupy shallow water strata minimized predation from deep-water predators, such as *Chaoborus*. (2) *D. laevis* tended to be larger than *D. pulex* from the end of July to mid-August 1978. The effect of small-size selective predators (such as *Chaoborus*) was, consequently, greater on the *D. pulex* population than on the *D. laevis* population. (3) Notonectid and large *Anax* predation rates were lower on *D. laevis* than on similarly sized *D. pulex*. In the vegetated habitat, *Buenoa* predation accounted for 6–20% of the predator-induced *D. pulex* mortality and 0.5–4.0% of the predator-induced *D. laevis* mortality. The proportions of predator-induced mortalities attributable to other predator species were not consistently different between the two prey species.

Total predation could not always account for total prey mortality in either *Daphnia* species (Figure 4). Predation could account for total *D. pulex* mortality on all dates only at Station 4. The proportions of *D. laevis* mortality attributable to predation showed few consistent trends across all sampling dates and stations. The impact of predation on the *D. laevis* population was largely determined by the size structure of the *D. laevis* population and the vertical distribution of the *D. laevis* population relative to the vertical distributions of predators. For both species, predation was of sporadic importance in controlling prey populations, and prey populations often cycled independently of predation intensity.

Competition experiments

We examined the effects of *D. pulex* and *D. laevis* on each other's population growth in two experiments. We conducted Experiment 1 in Bavarian Sausage Pond in 865 ml glass jars filled with filtered (52 μ) pond water and capped with 52 μ Nitex mesh. The initial conditions for each experimental treatment are described in Table V. Twice a week the contents of each jar were filtered through 52 μ mesh, each jar was refilled with filtered pond water, the experimental animals were returned to the jars, and the jars were re-immersed in the pond. Handling caused negligible mortality in this experiment. We preserved experimental daphnids with 95% ethanol at the end of the experimental period (September 11–27, 1978). Number of juveniles, adults, and eggs were then counted.

We conducted Experiment 2 in the laboratory in 865 ml glass jars to more precisely monitor cladoceran population fluctuations during the experimental period. Experimental jars were placed under wide-spectrum Gro-Lux bulbs on a 12L:12D photoperiod. Experimental temperatures approximated temperatures at the pond's surface during summer (21–22°C). Pond water filtered through 52 μ

mesh provided a natural food supply, and this medium was changed twice a week. The initial conditions of each experimental treatment (*D. pulex* control, *D. laevis* control, *D. pulex* + *D. laevis*, and both species + *Chaoborus*) are described in Table V. We examined the entire contents of each jar every three days for the first week and a half, and then at weekly intervals. We recorded number of juveniles, number of adult parthenogenetic females, and number of eggs carried by each parthenogenetic ovigerous female. *Chaoborus* larvae were replaced in jars where they had pupated, and extermination of either prey species in the *Chaoborus* trials resulted in the elimination of that replicate from the experiment. Total duration of this experiment was 37 days.

There were no significant differences between control and experimental treatments for any of the population parameters measured for either *D. pulex* or *D. laevis* in Experiment 1. There were, however, significant differences in population parameters between species (Table VI). *D. pulex* had significantly greater numbers of adults, average number of eggs per female, and birth rates (*b*) than *D. laevis* at the end of the 16 day trial period. There was a tendency for total *D. pulex* numbers to be greater than total *D. laevis* numbers at the end of the experiment, and the birth rate data indicates that *D. pulex* population growth would have outstripped *D. laevis* population growth if the experiment had been continued.

On the day after the initiation of Experiment 2, the experimental jars were examined for potential *Daphnia* mortality. Large proportions of the *D. pulex* populations had died, with only 3–6 *D. pulex* remaining in each jar. *D. laevis* populations, on the other hand, exhibited little initial mortality, and 16–20 *D. laevis* females remained in each jar to which they were added. Examination of jars following *Daphnia* counts on subsequent days revealed little handling mortality.

Despite this large initial bias in favor of *D. laevis*, *D. pulex* populations recovered and reached higher densities than *D. laevis* in both control and competition jars (Figure 6). After initial population peaks, *D. laevis* populations declined to near extinction in the competition jars, while maintaining a mean density of 100 individuals per jar in the control jars. After a low relative abundance of 12% in the competition jars, *D. pulex* populations increased steadily in relative frequency until they composed nearly 100% of total *Daphnia* numbers. It

Table V. Initial number of fourth instar *Chaoborus* larvae and young, adult female *D. pulex* and *D. laevis* added to each jar in each experimental treatment in Experiments 1 and 2. n is the number of replicates for each treatment.

Experiment	Treatment	No. <i>D. pulex</i>	No. <i>D. laevis</i>	No. <i>Chaoborus</i>	n
1	<i>D. pulex</i> control	5	0	0	5
	<i>D. laevis</i> control	0	5	0	4
	<i>D. pulex</i> + <i>D. laevis</i>	5	5	0	3
2	<i>D. pulex</i> control	20	0	0	6
	<i>D. laevis</i> control	0	20	0	6
	<i>D. pulex</i> + <i>D. laevis</i>	20	20	0	6
	Both + <i>Chaoborus</i>	20	20	1	6

Table VI. Population parameters measured at the termination of Experiment 1.

	No. juveniles			No. adults			Avg. # eggs/♀			Max. # eggs/♀			b		
	C	E		C	E		C	E		C	E		C	E	
<i>D. laevis</i>	46.5 ± 8.5	43.7 ± 8.2		14.2 ± 1.9	15.7 ± 1.9		1.86 ± 0.20	1.16 ± 0.61		4.2 ± 0.9	3.7 ± 1.3		0.08 ± 0.03	0.06 ± 0.03	
<i>D. pulex</i>	62.4 ± 11.9	64.0 ± 9.2		22.8 ± 4.4 ^a	17.0 ± 8.5		3.49 ± 0.33 ^a	3.72 ± 1.19 ^b		14.5 ± 1.0 ^a	10.7 ± 4.8		0.17 ± 0.02 ^a	0.10 ± 0.03 ^b	

Numbers represent the mean ± standard error for each experimental treatment. C = control treatment (*D. pulex* monocultures or *D. laevis* monocultures), E = experimental treatment (*D. pulex* + *D. laevis*, see Table IV). ^aSignificant difference between *D. laevis* and *D. pulex* values ($p < 0.05$, Wilcoxon rank sum test). ^bDenotes *D. pulex* values consistently higher than *D. laevis* values for all experimental replicates, but insufficient replication for statistical tests.

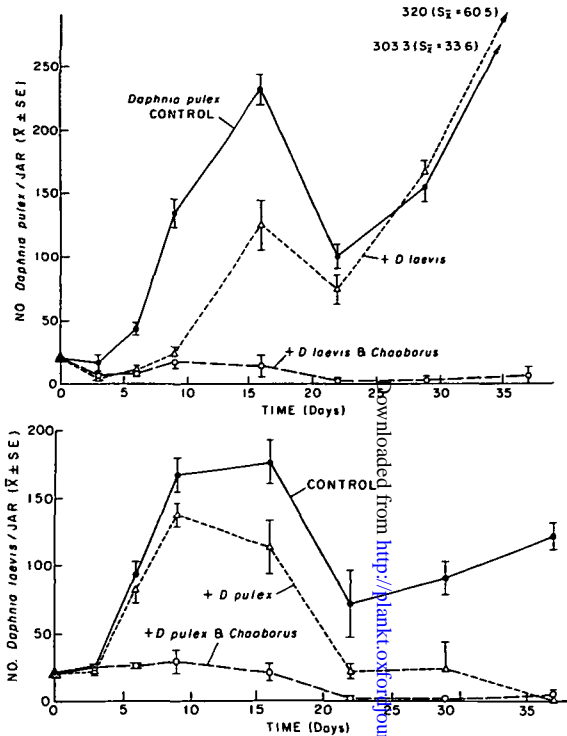


Fig. 6. Population fluctuations of *Daphnia pulex* (top) and *D. laevis* (bottom) in each set of treatment jars over time in Experiment 2. Error bars represent standard errors around the mean.

is apparent that *D. pulex* populations had a significant impact on *D. laevis* populations in the competition trials. *D. laevis* had a significant inhibitory effect on *D. pulex* population growth at the beginning of the experiment (Figure 6).

In control and competition trials, population numbers and birth rates of *D. pulex* and *D. laevis* showed similar fluctuations (Figures 6 and 7). The initial lags in *D. pulex* population growth in both competition and control trials were attributable to relatively low initial birth rates. Initial *D. pulex* birth rates were significantly lower in the competition than in the control trials, and *D. pulex* death rates were significantly higher in the competition than in the control trials on the subsequent sampling date (Figure 7). These results suggest that *D. laevis*'s initial inhibitory effect on *D. pulex* populations acted through initial *D. pulex* birth rate reductions, and subsequent *D. pulex* death rate increases. The retardation of *D. pulex* population development in the competition relative to the control trials resulted in a lack of synchrony between competition and control trials. This asynchrony (time lag effect) probably accounted for later differences in the juvenile to adult ratios, birth rates, and death rates of *D. pulex* populations in control and competition jars.

The decline in *D. laevis* population levels in competition relative to control trials, between the 16th and 22nd days after the initiation of the experiment, was

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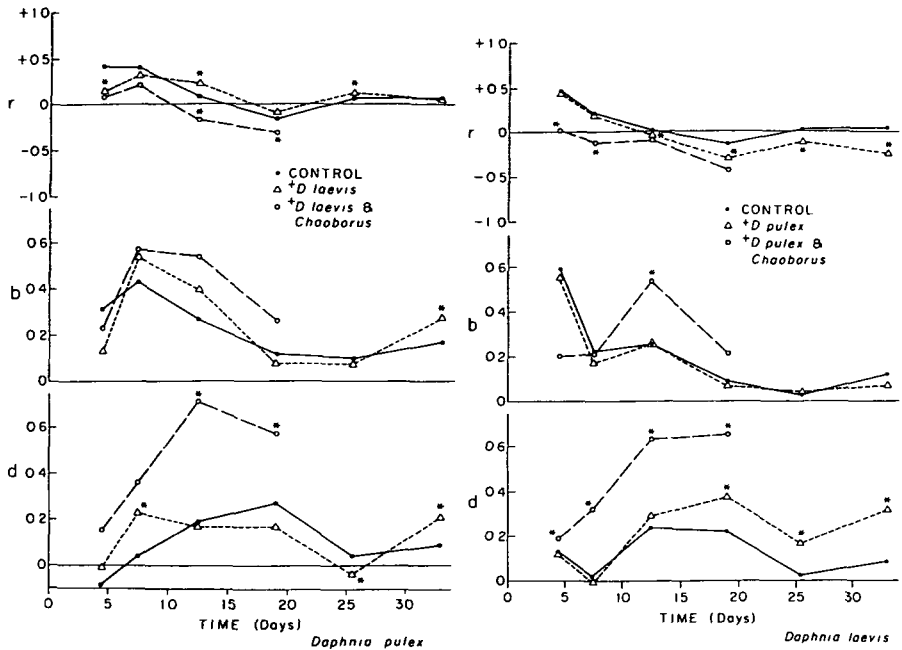


Fig. 7. Changes in mean population growth rates (r), birth rates (b), and death rates (d) for *D. pulex* (left) and *D. laevis* (right) in each set of experimental trials over time. Asterisks denote significant differences between values obtained from competition and control jars if located next to competition trial means, or between values obtained from competition and *Chaoborus* jars if located next to *Chaoborus* trial means ($p < 0.05$, Wilcoxon rank sum test).

associated with significant decreases in the mean number of eggs carried by each adult female and significant increases in the population death rates (Figures 7 and 8). The subsequent *D. laevis* declines to extinction in five of six competition jars (2 *D. laevis* remained in the 6th jar) were characterized by low *D. laevis* birth rates and significantly higher death rates in the competition relative to control jars. *D. pulex* may competitively exclude *D. laevis* by reducing the latter's birth rate and, especially, by increasing the latter's death rate.

Chaoborus predation kept both species at low, constant levels (Figure 6). Because of high initial handling mortality, *D. pulex* comprised only 15 to 20% of initial *Daphnia* numbers in the *Chaoborus* trials. Subsequently, the relative abundance of *D. pulex* fluctuated between 10 and 45% of total *Daphnia* numbers through the first 16 experimental days in the *Chaoborus* trials. *Chaoborus* predation caused the extinction of at least one *Daphnia* species in each of 5 experimental jars by the 22nd day. There was no indication of preferential elimination of either species by *Chaoborus*. *D. laevis* became extinct in one jar (between the 6th and 9th days), *D. pulex* became extinct in three jars (one between the 9th and 16th days, two between the 15th and 22nd days), and both species disappeared from a fifth jar (between the 16th and 22nd days). *Daphnia* spp. death rates were usually significantly higher in *Chaoborus* trials than in competition trials (Figure 7). In addition, there was a tendency for *Daphnia* spp. birth rates to be higher in

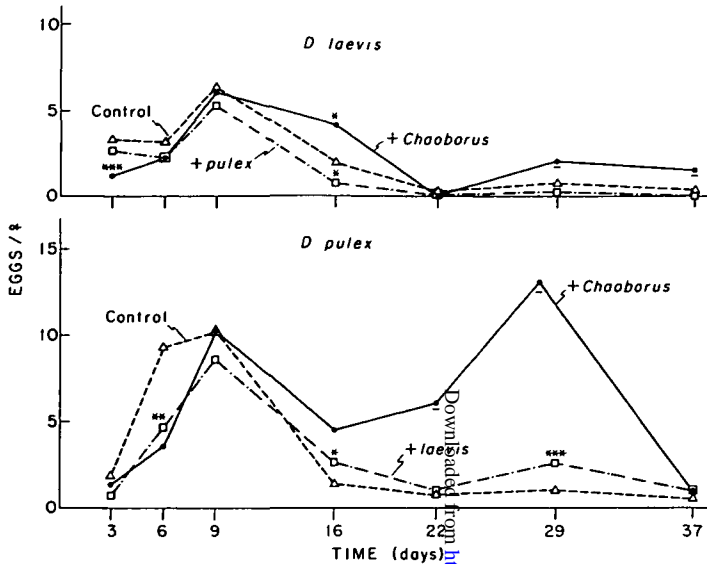


Fig. 8. Changes in the mean number of eggs carried by each adult female for *D. laevis* (top graph) and *D. pulex* (bottom graph) in each set of experimental trials over time. Asterisks denote significant differences between values obtained from competition and control jars if located next to competition trial means, or between values obtained from competition and *Chaoborus* jars if located next to *Chaoborus* trial means (* = $p < 0.05$, ** = $p < 0.025$, *** = $p < 0.01$, Wilcoxon rank sum test). A bar (-) means that only one treatment replicate remains in the *Chaoborus* trials.

Chaoborus trials than in competition trials ($p < 0.05$, for *D. laevis* on day 13; $p < 0.10$ for *D. laevis* on day 19 and for *D. pulex* on day 19; Wilcoxon rank sum test; Figure 7). These results suggest that *Chaoborus* predation was sufficient to balance *Daphnia* recruitment rates. Nevertheless, since *Daphnia* spp. declines in the *Chaoborus* jars paralleled *Daphnia* declines in other treatments, food abundance was probably important in determining the relative impact of *Chaoborus* predation. Neither *Daphnia* species was definitely superior in the *Chaoborus* trials.

As in Experiment 1, *D. pulex* reached higher population levels than *D. laevis*, and *D. pulex*'s individual fecundity was generally higher than *D. laevis*'s fecundity. Death rates were significantly higher for *D. laevis* than for *D. pulex* and birth and growth rates were significantly higher for *D. pulex* than for *D. laevis* in the competition jars near experiment termination. No significant population parameter differences between species were observed in the *Chaoborus* trials. The range of birth rate, death rate, and growth rate values recorded for both species were similar.

Ehippial females of both species were present in very low numbers in all treatments through the ninth day. After the ninth day no *D. laevis* ehippial females were found. Prior to the last sampling date, ehippial females usually accounted for less than 3% of total *D. pulex* adult females. On the last sampling date, however, substantial numbers (up to 31 jar⁻¹) of *D. pulex* ehippial females were found in some control and competition jars (0–44% of *D. pulex*

females). Male *Daphnia* were only rarely collected from experimental cultures.

In summary, *D. laevis* became extinct in jars where it was paired with *D. pulex*, but maintained densities of more than 100 l^{-1} in control monocultures. After an initial lag in population growth, *D. pulex* populations reached and remained at high levels ($75\text{--}320$ individuals jar^{-1}) in control and competition jars. At different times, each *Daphnia* species significantly decreased the birth rate and increased the death rate of the other species. *Chaoborus* predation kept both species at low levels.

Discussion

Year to year changes in the abundance of *D. laevis*, *D. pulex*, and their predators, and the results of predation trials indicate that *D. laevis*'s success from 1977–79 in this pond was largely dependent on the intensity of *Buenoa* predation. When *Buenoa* density was high, *D. laevis* was the dominant *Daphnia* species, and when the intensity of *Buenoa* predation was low, *D. pulex* was the dominant *Daphnia* species. In addition, *D. laevis*'s appearance in vegetated areas of the pond in 1978 coincided with *Buenoa*'s appearance in those areas, and *D. laevis*'s relative abundance was highest in those habitats where *Buenoa* was present. *Notonecta* and large *Anax* naiads may have had similar effects, but their preferences for *D. pulex* over *D. laevis* were less pronounced.

The physical structure of the pond was an important determinant of the intensity of macroinvertebrate predation. The analyses of the impact of predation showed that predation was minimized in 1978 by the spatial segregation of predators and prey. Since most hemipteran predators were associated with surface strata and odonate predators were generally restricted to the vegetated habitat, the effect of these predators on *D. pulex* populations was minimized by *D. pulex*'s occurrence in deep strata of open water areas. Low water levels in 1979 eliminated this spatial refuge for *D. pulex*, and resultant increases in the intensity of notonectid predation may have accounted for *D. laevis*'s complete dominance in that year.

Chaoborus larvae demonstrated no consistent preference for either *Daphnia* species, and the outcomes of long-term *Chaoborus* trials were not predictable. In natural systems, *Chaoborus* predation may allow the existence of these two *Daphnia* species by alleviating their competition for food. Since *Daphnia* egg production is primarily dependent on food supplies (Hall, 1964), this contention was supported by the observation that both *Daphnia* species tended to exhibit higher birth rates in jars where *Chaoborus* was present than in jars where *Chaoborus* were absent. *Chaoborus* predation kept both *Daphnia* species at low, constant levels in *Chaoborus* trials, effectively balancing *Daphnia* recruitment rates.

In 1978, cladocerans were subjected to predation from both *Chaoborus* larvae and macroinvertebrates. Differences in the vertical distributions and prey-size selectivities of these two types of predators may have accounted for differences in the vertical distribution and sizes of the two *Daphnia* species. *Chaoborus* larvae were most abundant in deep strata, and they exhibited a preference for small prey ($0.5\text{--}1.0$ mm, Cooper, 1979). Notonectid predators, on the other hand, preferred larger cladocerans and were associated with surface strata (Cooper, 1979). In

addition, notonectids exhibited a decided preference for *D. pulex* over *D. laevis*. Given these considerations, we might expect *D. laevis* to occur in shallower water strata and be larger than *D. pulex* if these predators have a significant effect on *Daphnia* populations. While the data are limited, predicted differences in the vertical distribution of these two *Daphnia* species were often observed in 1978, and predicted size differences between these two prey species were observed in late July 1978. Mortality attributed to *Chaoborus* predation was significantly higher for *D. pulex* than for *D. laevis*, primarily because *D. laevis* populations occupied shallower water strata than *D. pulex* populations, and, secondarily, because *D. laevis* was occasionally larger than *D. pulex*. *D. pulex* may have been excluded from these refuges from *Chaoborus* predation due to the vulnerability of large *D. pulex* to notonectid predation. It is perhaps significant that, when a large range of *D. pulex* sizes were present, young *D. pulex* occurred in surface strata and larger adults were found in deeper strata. In small laboratory aquaria, these two *Daphnia* species exhibited similar differences in vertical distribution.

The analyses of the impact of predation suggest that predation could account for all of the *D. pulex* mortality at the vegetated stations, but could not account for all of the *Daphnia* spp. mortality at other stations, especially if there were large population declines. Cooper (1979) and Smith and Cooper (in press) argue that peaks occurred because prey populations outstripped predator control. Subsequent prey declines were due to the depletion of the cladoceran food supply.

In the long-term experiments *D. laevis* and *D. pulex* exhibited large initial increases in population numbers, presumably when food resources were abundant. Data presented in Smith and Cooper (in press) indicate peak algae abundances during the time that Experiment 1 was conducted. *D. pulex* and *D. laevis* co-existed for the 16-day trial period, although *D. pulex* tended to have higher population growth rates. In the second competition experiment, *D. pulex*'s initial inhibitory effect on *D. laevis* populations occurred when *Daphnia* populations in all treatments were exhibiting large declines, suggesting a decrease in food resource levels. *D. pulex* populations subsequently increased in competition jars, but *D. laevis* populations became extinct, primarily as a result of increased death rates. These results suggest that these two *Daphnia* species may co-exist when food levels are high, but that *D. pulex* will dominate when food resources become limited. Food resources (phytoplankton) may remain at high levels due to intense predation on consumer species or high inputs of nutrients. The appearance and increase of *D. laevis* populations in open water areas coincided with large population increases for *D. pulex*. When these two *Daphnia* species co-existed in open water areas, growth rates, birth rates, and death rates of both species were similar, and *D. laevis*'s relative abundance remained relatively constant (1% of *Daphnia* numbers). Significant positive correlations between the abundances of these two *Daphnia* species suggest that they were responding to similar factors. *D. laevis*'s absence from open water areas in July was perhaps due to *D. pulex*'s competitive superiority when food levels were low in early July, followed by the control of cladoceran populations by a combination of low food levels and *Chaoborus* predation which kept both species at low levels (undetectable levels

for *D. laevis*). *D. laevis* appeared when prey populations had presumably escaped from predator control, largely as a result of increased prey birth rates (Table II). For example, number of eggs per mature female *D. pulex* increased from 0 to 3.85 at Station 2 and from 0 to 0.62 at Station 5 between August 14 and August 25, 1978. Both species declined after population peaks due to depletion of their common food supply (Cooper, 1979; Smith and Cooper, in press).

D. laevis densities were negatively correlated with *D. pulex* densities in the vegetated and interface habitats, suggesting that quite different processes were occurring in the vegetated and open water habitats. *D. laevis* first appeared in the vegetated habitat, and its subsequent relative abundance was highest there. Since macroinvertebrate predation was much more intense in the vegetated habitat than in other deep-water habitats, selective macroinvertebrate predation on *D. pulex* may have accounted for *D. laevis*'s relative success in the vegetated habitat. Predation in the vegetated habitat may have been more than sufficient to offset the low birth rates recorded for *D. pulex* in that habitat. Co-existence of these two species in the vegetated habitat may have been mediated, therefore, by selective macroinvertebrate predation on the competitively-superior *D. pulex*.

The results of this study contribute to a growing body of evidence which indicates that the distributions and abundances of different cladoceran species (or varieties) are controlled by selective predation. Where large-size selective visual predators, such as fish and salamanders, are abundant, small-bodied cladoceran species dominate; where small-size selective invertebrate predation is intense, large-bodied cladocerans dominate (Brooks and Dodson, 1965; Galbraith, 1967; Wells, 1970; Dodson, 1970, 1974a). Exuberant cladocerans are often most abundant where the intensity of predation by both large and small-size selective predators is high (O'Brien *et al.*, 1979). The exuberant, diaphanous structures of these species may frustrate the attack and handling tactics of invertebrate predators, while minimizing their apparent size to visual, vertebrate predators (Dodson, 1974b; Kerfoot, 1975, 1977a; O'Brien *et al.*, 1979). In addition, exuberant morphs may minimize predation by having considerable escape abilities (O'Brien and Vinyard, 1978; Jacobs, 1966). The wide-spread observation that exuberant cladoceran species dominate in predator-rich environments, while non-exuberant cladoceran species dominant in predator-free environments may be due to the efficient escape responses of exuberant forms (Green, 1967; Jacobs, 1977, 1978; O'Brien and Vinyard, 1978; Zaret, 1972a, 1972b).

The abundances of two *Daphnia* species in this pond were apparently controlled by similar factors. The relative dominance of *D. laevis* and *D. pulex* in the face of intense *Chaoborus* predation was dependent on the abundance of macroinvertebrate (especially notonectid) predators. *D. laevis* dominated when notonectid predation was intense, owing to its efficient escape response to notonectid attack. Because of its superior competitive abilities, *D. pulex* dominated where notonectid influence was limited. Small-size selective *Chaoborus* predation was important in controlling the densities of a third competitor, *Ceriodaphnia affinis*, but had less of an effect on *Daphnia* spp. because of their large, adult sizes (Cooper, 1979).

The results of this study also underscore the importance of competition to

zooplankton community structure. The dominance of *D. pulex* in 1977 and 1978 demonstrate that, for the greater part of the sampling period, field dynamics were consistent with the results of the competition experiments. Our results and the results of other recent studies suggest that the importance of competition to zooplankton community structure should be reevaluated (Jacobs, 1978; Neill, 1975; Lynch, 1979; Smith and Cooper, in press).

Our work illustrates that simple explanations for such complex phenomena as community structure are inappropriate. The relative abundances of these two *Daphnia* species were controlled by a complex mosaic of factors which varied through time and space. Selective predation by notonectids could, apparently, overwhelm the competitive superiority of *D. pulex*. At other times, however, the effect of predation was minimal, and resource depression and competition were of paramount importance.

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