



Effects of an Organophosphorus Insecticide on the Phytoplankton, Zooplankton, and Insect Populations of Fresh-Water Ponds

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EFFECTS OF AN ORGANOPHOSPHORUS INSECTICIDE ON THE PHYTOPLANKTON, ZOOPLANKTON, AND INSECT POPULATIONS OF FRESH-WATER PONDS¹

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ABSTRACT

Dursban, an organophosphorus insecticide, was applied on June 3, June 18, and July 1 to eight shallow (24 cm) experimental ponds near Bakersfield, California. Four ponds were treated at 0.028 kg/ha (= 0.025 lb./acre), four were treated at 0.28 kg/ha, and four were kept as controls. Phytoplankton, zooplankton, and insect populations were sampled on 21 dates between May 20 and August 16. Insect larvae and nymphs were more reduced in numbers than were insect adults, reflecting in part the ability of the latter to emigrate and immigrate. Twenty-four-hour posttreatment samples for the second and third, but not first, treatments showed greater reductions of predaceous (Notonectidae, Dytiscidae, Coenagrionidae, larval Hydrophilidae) than of "herbivorous" (Corixidae, Baetidae, adult Hydrophilidae) insect populations. Predaceous insect populations generally recovered to control-pond levels more slowly than herbivorous insect populations. Five weeks after the last insecticide treatment, predaceous insects averaged only 45% and 9% as abundant in low dose and high dose ponds, respectively, as they were in control ponds ($P < 0.02$); corresponding figures for herbivorous insects were 108% and 206% ($P < 0.10$). Initially, *Cyclops vernalis* and *Moina micrura* were the only crustacean zooplankters present, and both experienced high mortality due to treatments. Recovery in low dose ponds was variable, requiring 1–3 weeks, and in high dose ponds occurred only 3–6 weeks after the final treatment. Populations of *Diaptomus pallidus* seemed unaffected by the lower rate of treatment, but became large only after *Cyclops* populations had been reduced by the insecticide or other factors. *Ceriodaphnia* sp. became abundant in late July or early August in all four control ponds but not in any treated ponds. Herbivorous rotifers, principally in the genera *Brachionus*, *Polyarthra*, *Hexarthra*, *Filinia*, and *Tripleuchlanis*, increased dramatically, often five- to twentyfold, within 1–3 days after *Moina* and *Cyclops* populations were decimated by Dursban, but became abundant in control ponds only during the brief absence of *Moina* in early July. All planktonic rotifers, except *Polyarthra*, were more abundant in treated than in control ponds; all benthic-littoral rotifers (e.g., *Lecane*, *Monostyle*, *Tripleuchlanis*, *Platyiias*, *Lepadella*, *Testudinella*) were more abundant in control than in treated ponds. The predaceous rotifer *Asplanchna brightwelli* was 35 times more abundant in treated than in control ponds, feeding primarily on herbivorous rotifers, sometimes on *Cyclops*, *Diaptomus*, *Moina*, and large algae, and rarely on small mayfly (Baetidae) nymphs and chironomid larvae. *Asplanchna* populations were composed of three morphotypes, ampulliform, cruciform, and campanuliform, the last of which tended to be highly cannibalistic. The "wings" of humps of the cruciform morphotype apparently represent a mechanism for minimizing such cannibalism. The reduction of herbivorous crustaceans by Dursban and the restraint of herbivorous rotifers by *Asplanchna* predation permitted the rapid increase of phytoplankton populations in treated ponds and, even 6 weeks after the last treatment, the phytoplankton was two and 16 times more abundant in low dose

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and high dose ponds, respectively, than in control ponds. Blooms of bluegreen algae (*Anabaena*, *Anabaenopsis*) developed in three high dose and one low dose pond, and a bloom of the diatom *Synedra* developed in one low dose pond. The long-spined alga *Schroederia setigera* seemed favored by high *Moina* and *Diaptomus* populations and low *Cyclops* populations. The significance of these results for insect-control programs is discussed.

INTRODUCTION

The influx of pesticides into fresh-water environments is increasing throughout the world with uncertain long-term effects on aquatic ecosystems and with frequently severe damage to vertebrate wildlife in particular. In the United States, 1968 production of synthetic organic pesticides was 1.2 billion pounds, an increase of 14% over the preceding year; and, in this same year, United States' exports of these pesticides increased by 23% (Fowler, Mahan, and Shepard 1970). Insecticides compose slightly more than one-half of this production and are applied to 5% of the total area of the 48 states at an average annual rate of approximately 4.5 kg/ha (President's Science Advisory Committee 1963, Frear 1968, Fowler et al. 1970). Some insecticide is applied directly to aquatic environments to temporarily reduce populations of mosquitoes, blackflies, and chironomid and chironomid midges. Larger amounts enter aquatic systems in runoff water from agricultural land, or as a result of discharge of industrial wastes into streams and rivers by pesticide manufacturers and formulators (Nicholson 1967), or by the settling out of airborne, insecticide-contaminated dust (Risebrough et al. 1968). Whatever the mode of transport and introduction, these insecticides have a multiplicity of undesirable effects (see reviews by Bauer 1961, Rudd 1964, Cope 1965, Stickel 1967, Johnson 1968).

Among the least studied effects of insecticides are those on the population dynamics of aquatic plants and animals. Rarely have experiments assessed the influence of an insecticide on competitive, plant-herbivore, or prey-predator interactions of aquatic populations. The present study documents such influences as they were demonstrated by phytoplankton and invertebrate populations of small fresh-water ponds treated with the insecticide Dursban. This study was stimulated primarily by earlier observations (Hurlbert et al. 1970) of large unexplained increases in populations of the copepod *Diaptomus pallidus* and the predaceous rotifer *Asplanchna brightwelli* after treatment of ponds with this insecticide.

METHODS AND MATERIALS

Insecticide

Dursban (0,0-diethyl 0-3,5,6,-trichloro-2 pyridyl phosphorothioate) is an organophosphorus insecticide developed by Dow Chemical Company. It is presently registered for use against mosquitoes at 0.05 lb./acre

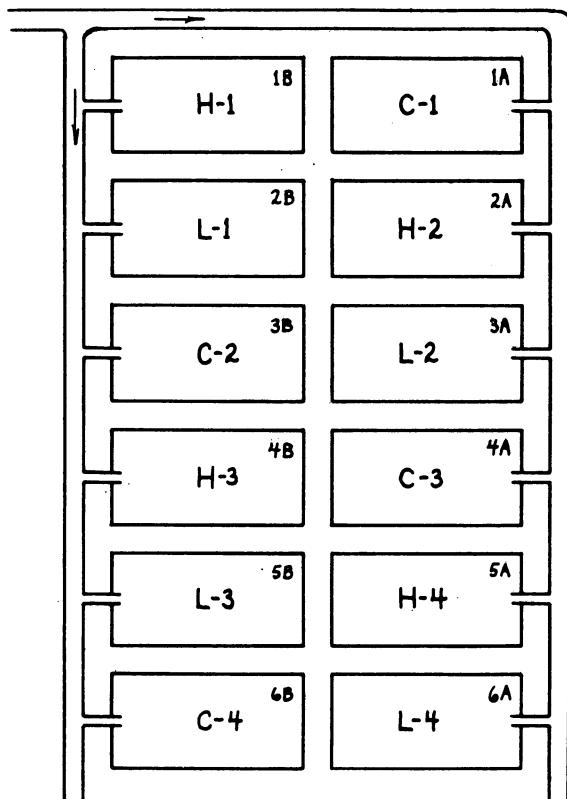


FIG. 1. Arrangement of experimental ponds. C = control pond, L = low dose pond (0.028 kg/ha), H = high dose pond (0.28 kg/ha). Numbers in upper right hand corners are those used in Hurlbert et al. (1970). Arrows show direction of water flow through ditches to the valved inlet pipes of the ponds.

(= 0.56 kg/ha) and has been tested at 0.1–0.2 lb./acre for control of chironomid midges. Dursban constituted about 2½ % of the approximately 320,000 lb. of insecticide applied for mosquito control in California in 1969 (California Mosquito Control Association 1970). Much of its value as an insecticide stems from its stability; it is more resistant to hydrolysis and oxidation (Dow Chemical Company 1967) and to microbial degradation (Hirakoso 1968) than are most organophosphorus insecticides. It is not subject to food-chain magnification, however, as it is rapidly degraded enzymatically in animal tissues.

Ponds and treatments

The experimental ponds, located 15 miles south of Bakersfield, Kern County, California, and consisting of shallow, unlined excavations measuring 8 m by 17 m, were maintained at a depth of about

24 cm by the addition of water from a nearby canal twice weekly; the zooplankton was sparse in this water. These ponds had been used for earlier investigations on the effects of organophosphorus insecticides (Keith and Mulla 1966, Hurlbert et al. 1970). Water temperatures were recorded with a Taylor maximum-minimum thermometer from May 21 to the end of June 1968. During the last week in May the mean daily maximum and minimum were 31°C and 19°C, respectively, and during the last week of June they were 35°C and 23°C. Water temperatures in the middle of the summer occasionally may have exceeded 37.8°C (100°F).

Ponds were arranged in two rows of six each (Fig. 1). Four ponds were kept as controls (C-1, 2, 3, 4), four (L-1, 2, 3, 4) were treated three times at 0.028 kg active ingredient/ha ($= 0.025 \text{ lb./acre} = 7.2 \text{ ppb}$), and four (H-1, 2, 3, 4) were treated at 0.28 kg/ha. Ponds were assigned to treatment levels in a manner designed to favor maximum between-pond variation within each treatment level. Two ponds in each row were assigned to each treatment level, and no two ponds in the same treatment level were adjacent (Fig. 1). If two ponds were very similar, they were assigned to different treatment levels. For example, ponds 1A and 1B, unlike the other 10, had not been flooded the previous year and were overgrown with grass; ponds 3A and 6B were similar in that they both received heavy insecticidal treatment the previous summer (four applications of Dursban at 1.12 kg/ha (Hurlbert et al. 1970)). Similarities in zooplankton were also determined from samples collected on May 28 and June 3.

Treatment dates were June 3, June 18, and July 1, 1968. An emulsifiable concentrate formulation (M-3019, 40% active ingredient) of the insecticide was diluted with water and applied with hand sprayers to the water surface at the rate of 75 liters/ha ($= 8 \text{ gal/acre}$).

Sampling regime and methods

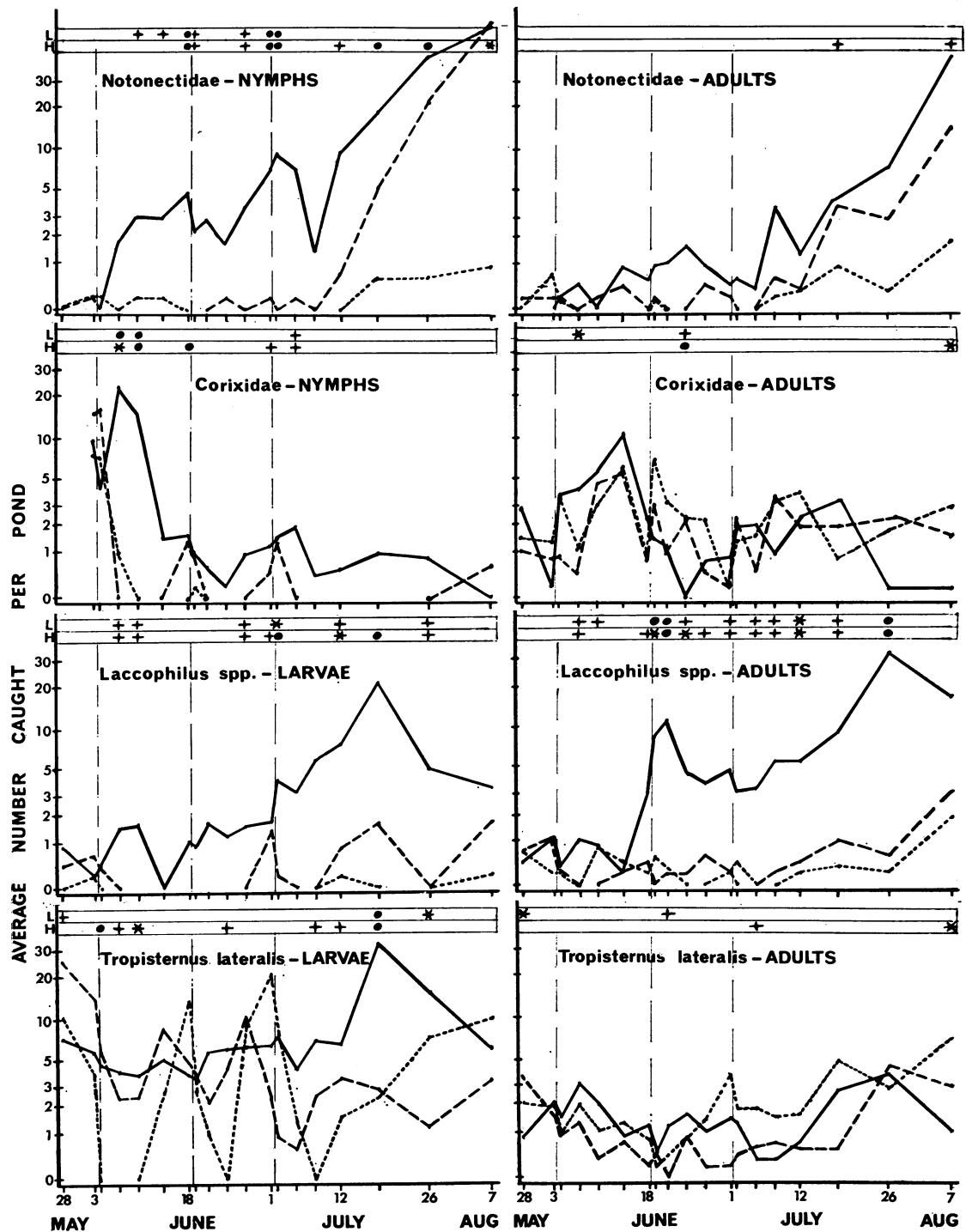
The ponds were flooded for the first time on May 18. Samples of phytoplankton and zooplankton were taken on May 20, 28; June 3, 4, 7, 10, 14, 18, 19, 21, 24, 28; July 1, 2, 5, 8, 12, 19, 26; and August 7 and 16 from each of the 12 ponds. Aquatic insects were also collected on these dates, with the exception of May 20 and August 16. The plankton and insect samples for June 3, 18, and July 1 were taken immediately before the Dursban treatments on those days. Samples usually were taken between 0800 and 1200 hr (PDST).

One 140-ml phytoplankton sample was collected with a plastic vial 6–10 cm beneath the surface of an area near the center of each pond. The sample was preserved by addition of 10 ml of 37% formalin

and allowed to settle for at least 2 weeks. Then 130 ml of clear water from the middle of the sample vial was drawn off leaving 20 ml of phytoplankton concentrate. (Siphoning from the middle of the water column was necessitated by the frequent presence of *Anabaena* and *Anabaenopsis* which floated rather than settled.) The concentrate was mixed by gently inverting the vial a few times; then a drop was removed and placed on a Spencer Bright-Line hemacytometer. The cells in 0.5 mm³ of concentrate (equivalent to 3.5 mm³ of pond water) were counted under a compound microscope at a magnification of 430 \times . Since the vertical dimension of the hemacytometer chamber was only 100 μ , larger algae, e.g. *Closteriopsis*, *Volvox*, and some *Anabaena*, were underrepresented in these counts. Therefore their abundances in the zooplankton samples also were estimated so that this underrepresentation would not pass unrecognized. Identifications of algae were made by using Prescott (1951, 1954) and Smith (1950).

Zooplankton samples were taken with a 15-cm-diameter plankton net, with mesh openings 40–50 μ across, to which was affixed a vial with a "window" of stainless steel screen with mesh openings of 74 μ . The net was mounted on a steel sled and rode about 2.5 cm from the pond bottom. Two samples were taken from each pond on each sampling date; the net was pulled parallel to and 3–4 m from each of the pond's shorter sides. The samples were preserved in 10% formalin. In the laboratory the two samples were combined and diluted to 100 ml. These 100 ml were agitated vigorously, and 4 ml were drawn off with a wide-mouthed (ca. 5-mm) eyecup for examination in a Sedgwick-Rafter counting chamber. The counting chamber had to be filled three or four times for complete examination of each 4-ml subsample, and each time we counted the copepod nauplii in three strips measuring 1,880 μ by 20 mm, the rotifers (except *Asplanchna*) in three strips measuring 1,880 μ by 50 mm, and all *Asplanchna* and all crustaceans (except nauplii). When in a particular sample a certain species was very abundant, that species was counted over a smaller area of the chamber and calculations adjusted accordingly. Crustaceans were identified with the use of Brooks (1959), Wilson (1959), Yeatman (1959), and Goulden (1968). Rotifers were identified by using Myers (1930), Ahlstrom (1940, 1943), Bartos (1948), Voigt (1956), Edmondson (1959), and Pourriot (1965a).

To study polymorphism and diet of *Asplanchna*, subsamples of *Asplanchna*-rich zooplankton samples were heated at just below the boiling point for 1–3 min in a 5% potassium hydroxide solution. This treatment caused *Asplanchna*, which contracted when killed by the formaldehyde, to expand to approximately its normal form and also cleared its tissues



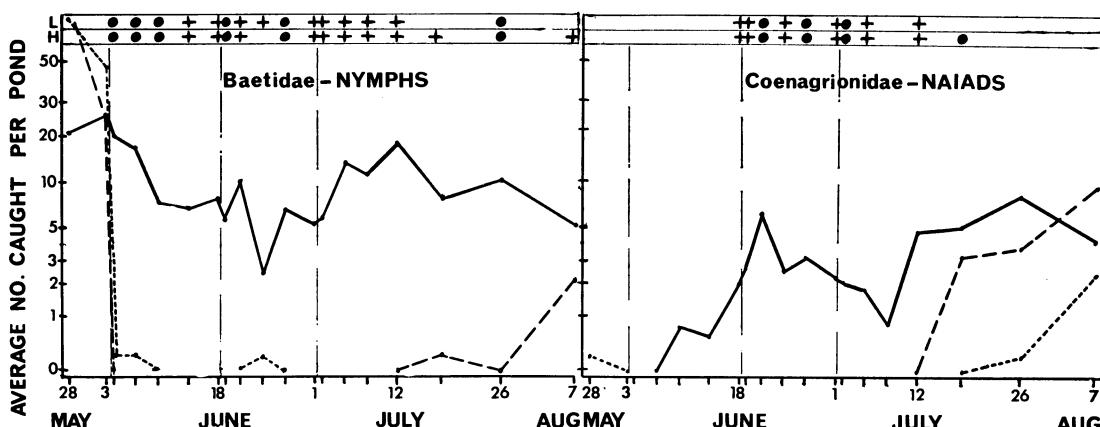


FIG. 2. Effects of insecticide treatment on the dominant insect populations. Geometric mean abundance of $n + 1$, where n is the number caught per pond, is represented as follows: solid line = control ponds; long dashes = low dose ponds; short dashes = high dose ponds. Vertical dashed lines indicate treatment dates. Symbols across top of each chart show the statistical significance, as determined by the Wilcoxon rank sum test (Wilcoxon and Wilcox 1964), of the difference between the control and the low dose ponds (L) and between the control and the high dose ponds (H). Significance levels denoted as follows: double asterisk, $P < 0.01$; solid dot, $0.01 < P \leq 0.02$; asterisk, $0.02 < P \leq 0.05$; plus sign, $0.05 < P \leq 0.10$; no symbol, $P > 0.10$.

permitting easy observation, identification, and enumeration of the stomach contents.

Insect samples were taken with a net having mesh openings of 500μ and a cross-sectional area of 680 cm^2 at the mouth. It was mounted on a steel sled and pulled at a distance of about 1 m from the edge, along the two long sides of each pond exactly as in our earlier study (Hurlbert et al. 1970). This method was adequate for many littoral and nektonic species, but less satisfactory for strictly benthic species. Material collected in the net was preserved in 95% ethanol. The insects were sorted, enumerated, and identified in the laboratory. Identifications were made with Usinger (1956).

RESULTS

Insect populations

The numbers of the more common insects in the experimental ponds were plotted according to insecticide treatment and date (Fig. 2). The family Notonectidae was represented by *Buenoa* spp. and *Notonecta* spp., and the family Corixidae primarily by *Corisella* spp. and occasionally by individuals of other genera. *Laccophilus* spp., small beetles 4–5 mm long, were the most common representatives of the Dytiscidae, and *Tropisternus lateralis*, about twice as long as *Laccophilus*, was the principal representative of the Hydrophilidae. Mayfly nymphs (Baetidae) and damselfly naiads (Coenagrionidae) were identified only to family. The May 28 data for corixid nymphs were lost.

The responses of insect populations to the insecticide treatment were correlated more closely with

their trophic level than their taxonomic positions. The predaceous notonectid and *Laccophilus* populations increased gradually with time in the control ponds and reached maxima toward the end of the experiment. In the treated ponds these predator populations were much reduced and even 5 weeks after the last treatment had not recovered to the level of the control-pond populations, except in the case of notonectid nymphs in the low dose ponds. A predaceous bug, *Belostoma* sp. (Belostomatidae: Hemiptera), was caught sporadically in three of the control ponds throughout the experiment; the largest number recorded was 82 nymphs and adults caught in C-1 on August 7. It was found only in H-4 of the high dose ponds, but not after June 10. *Belostoma* was initially present in all low dose ponds, but disappeared from them shortly after the first or second treatment; by August 7 it had reappeared in three of them. Miscellaneous dytiscids, predominantly *Rhantus* sp. and *Dytiscus* sp., were caught in small numbers in most ponds initially and in large numbers in C-1 (26 larvae, July 19) and C-4 (37 larvae, August 7). They were not caught in high dose ponds after the first treatment. In low dose ponds they recovered from the first two treatments by June 28, but were never caught following the third treatment. Cranefly larvae (Tipulidae: Diptera), initially absent from all pools, never were caught (except for one individual) in any of the treated ponds, but were occasionally caught in large numbers in three of the control ponds (maxima: 33 in C-1, July 26; 88 in C-2, July 19; 24 in C-4, June 28). Damselfly naiads (Fig. 2), also initially absent from all ponds (except for one individual in H-2), had developed moderate

populations in all control ponds by the end of June, but were not caught at all in any of the treated ponds until 3–4 weeks after the last treatment, when their populations developed rapidly.

Trends in corixid populations were just the reverse of those shown by notonectids and *Laccophilus* (Fig. 2). In control ponds the corixids were most numerous 2–3 weeks after flooding and declined to minima on June 24 and August 7. In the treated ponds corixid nymphs declined to zero with each treatment, but recovered within 2 weeks, except after the third treatment; on August 7 corixid nymphs were caught in only one of the eight treated ponds. Adult corixids showed few negative effects of treatment and were more numerous in high dose than in control ponds on June 24 and August 7. At the other extreme, mayfly nymphs (Fig. 2), persisting in control ponds in good numbers throughout the experiment, were decimated by the first treatment of low and high dose ponds and showed little sign of recovery until August 7, when moderate numbers were caught in two of the low dose ponds.

Tropisternus adults, like corixid adults, showed little effect of insecticide treatment except that they were significantly more numerous in the high dose than in the control ponds on August 7 (Fig. 2). Adult populations of another hydrophilid, *Helophorus* sp., behaved similarly and on the average were

larger on July 19 and 26 and August 7 in the high dose ponds than in either control or low dose ponds. *Tropisternus* larvae were well represented in all ponds a week after flooding and attained maximum abundance in each control pond sometime between July 8 and July 26 (Fig. 2). They recovered well from the first and second insecticide treatments, but required approximately a month after the third treatment to approach abundances comparable to those of the control ponds.

Predaceous versus herbivorous insects

Predaceous insects were considered to include hydrophilid larvae and all dytiscids, notonectids, odonates, tipulids, and belastomatids. Herbivorous insects were considered to include hydrophilid adults and all corixids and mayflies. Strictly speaking, many of these so-called "herbivores" are omnivores, capable of feeding on protozoa, rotifers, and other microfauna (Pennak 1953, Usinger 1956). Responses of predaceous and herbivorous insect populations were strikingly different (Fig. 3). In control ponds the total number of predaceous insects increased more or less continuously throughout the experiment. In the same ponds the herbivorous insects were initially rather abundant, decreased to a minimum in late June, and thereafter fluctuated somewhat irregularly.

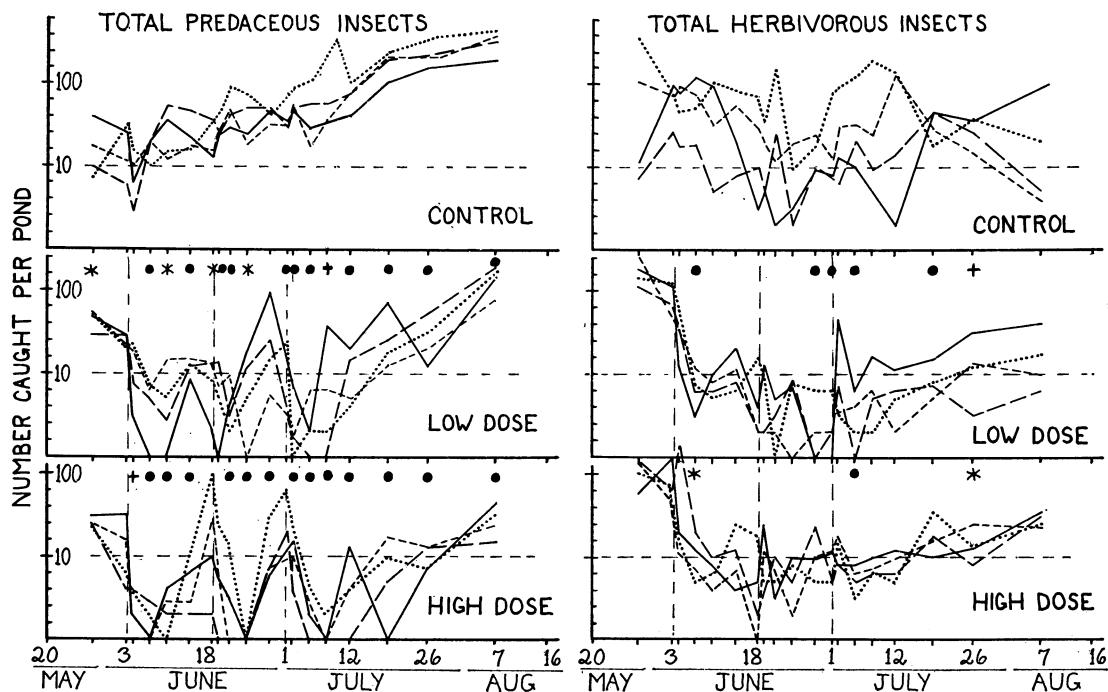


FIG. 3. Effects of insecticide treatments on the total predaceous and total herbivorous insect populations. Statistical significance determined by the Wilcoxon rank sum test and denoted as in Fig. 2. Individual ponds represented as follows: dotted line = C-1, L-1, H-1; short dashes = C-2, L-2, H-2; long dashes = C-3, L-3, H-3; solid line = C-4, L-4, H-4. Because the May 28 data for corixid nymphs were lost, the number of herbivorous insects is underestimated for all ponds on that date.

In treated ponds the first insecticide application caused about the same mortality (ca. 40–90%) to predaceous and herbivorous insects. Subsequent treatments caused similar reductions in the total number of predaceous insects, but in most cases statistically indetectable effects on total numbers of herbivorous insects. Up until June 18 herbivorous insects were more abundant on the average in low dose than in high dose ponds, but on every sampling date thereafter they were more abundant in high dose ponds, although never significantly so. Although on cessation of treatments per capita rates of increase were higher in total predaceous insects (as indicated by slopes of the lines in Fig. 3) than in total herbivorous insects, 5 weeks after the last treatment predaceous insects nevertheless were significantly less abundant and herbivorous insects slightly (but non-significantly) more abundant in treated than in control ponds. On August 7 the mean numbers of predaceous insects caught at different treatment levels were 303, 135, and 26 in control, low dose, and high dose ponds, respectively; corresponding values for herbivorous insects were 13, 14, and 28.

At least two factors account for the relatively mild effects of the second and third treatments on total herbivorous insects. First, the most sensitive herbivores, the mayflies, were so thoroughly eliminated by the first treatment that none were left to die in response to subsequent treatments (Fig. 2). Second, the dominant herbivores (corixids and *Tropisternus* adults) at the time of the subsequent treatments probably (1) absorbed or ingested less insecticide, (2) were physiologically more tolerant of it, or (3) recolonized treated ponds more rapidly than did the dominant predators (notonectids and *Laccophilus* adults). With respect to this last possibility, the ability to fly from other localities certainly was a factor in maintaining adult corixid populations in high dose ponds, since, as evidenced by the absence of nymphs, corixids did not reproduce in those ponds subsequent to the first treatment (Fig. 2). In general, recovery of all insect populations might have been less rapid had there not been four control ponds serving as a source of colonists for treated ponds.

The less severe long-term effects on herbivorous than on predaceous insects are readily explained. For herbivorous insects the insecticide treatments partially replaced one mortality factor (predaceous insects) by another (Dursban), whereas for predaceous insects the treatments represented an additional mortality factor. This assumes that the dominant predators were not limited by cannibalism or by predation by other species. Furthermore, although treatments reduced, at least temporarily, the food supply of predaceous insects (i.e., crustaceans and herbivorous insects), they caused increases in phyto-

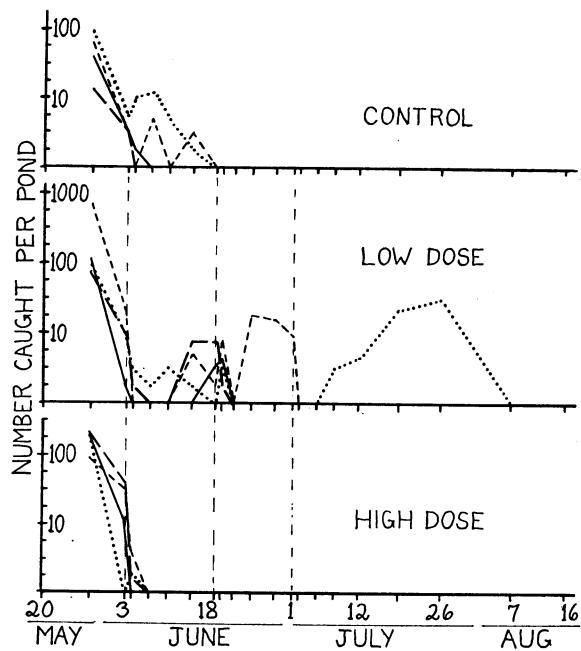


FIG. 4. Effect of insecticide treatment on populations of the tadpole shrimp *Triops longicaudatus* LeConte (Notostreaca:Crustacea). Individual ponds represented as in Fig. 3.

plankton (Fig. 7) and presumably in the food supply of herbivorous insects.

Tadpole shrimp

Previous observations showed that whenever the experimental ponds were flooded during a warm part of the year, large numbers of the tadpole shrimp, *Triops longicaudatus*, suddenly appeared and then gradually disappeared over a period of a few weeks. In the present experiment they appeared, as expected, soon after flooding of the ponds on May 18, and by June 3, date of the first treatment, they were already declining rapidly in all ponds (Fig. 4). The first treatment apparently killed all tadpole shrimp in the high dose ponds, but in all four low dose ponds they persisted until at least June 19.

Of special interest were the tadpole shrimp that appeared in pond L-1 beginning June 24. These were small, apparently recently hatched individuals and clearly not survivors of the tadpole shrimp generation that hatched on May 18 or shortly thereafter. Since the second generation normally does not hatch until a pond is dried up and then reflooded, apparently the secondary hatch was somehow caused by the low dose insecticide treatment. This possibility merits further study. Throughout its worldwide distribution this crustacean can damage young rice seedlings both by feeding on them and by stirring up bottom sediments and decreasing light availability (Rosenberg 1947, Longhurst 1955, Grigarick, Lange,

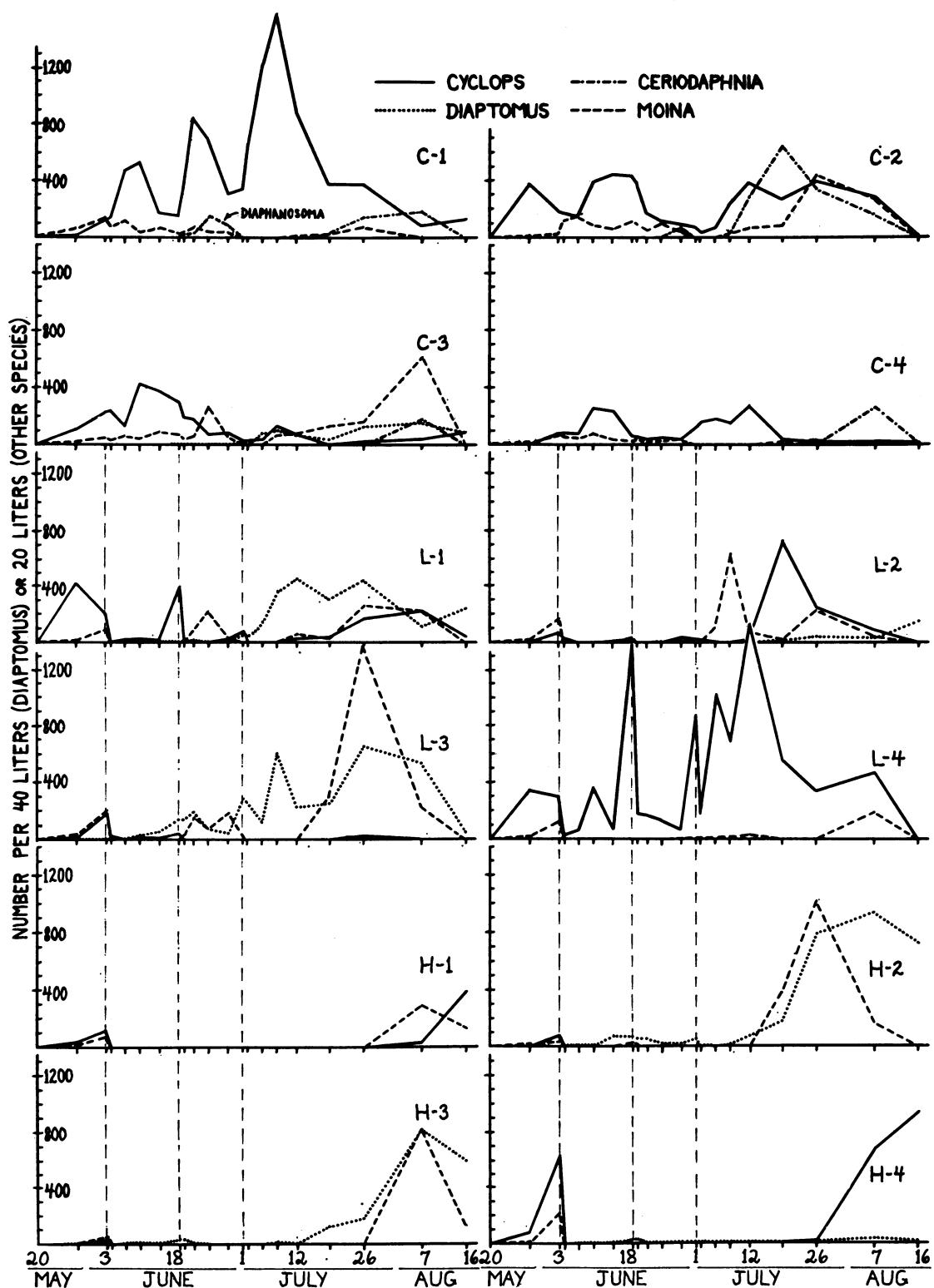


FIG. 5. Effect of insecticide treatment on populations of planktonic crustaceans. Abundance of *Cyclops* and *Diaptomus* are exclusive of nauplius larvae.

and Finfrock 1961, Crossland 1965). Rice fields are frequently treated with insecticides to control either mosquitoes breeding there or insects attacking the rice.

Planktonic crustaceans

Five species of planktonic crustaceans occurred in the experimental ponds: two copepods, *Cyclops vernalis* Fischer and *Diaptomus pallidus* Herrick, and three cladocerans, *Moina micrura* Kurz, *Diaphanosoma brachyurum* (Liéven), and a species of *Ceriodaphnia*, either *C. pulchella* Sars or *C. quadrangula* (O. F. Müller). The abundances of these species are shown in Fig. 5 and the abundances of copepod nauplii in Fig. 6. These data, as well as those for the rotifer populations (Fig. 10 and 13), underestimate true population densities since, as a result of its very fine mesh, the plankton net undoubtedly operated with an efficiency of much less than 100%. The zooplankton data are presented by pond rather than by species because the numerical interrelations of the species can only be demonstrated in this way.

Moina was the only cladoceran present before the first treatment. In each control pond a small population developed during late May and June and then completely disappeared on July 1 and 2, although some *Moina* were present in four of the eight treated ponds on July 1. During July, *Moina* populations of control ponds increased again, especially in C-2 and C-3, and were joined by *Ceriodaphnia*, which on a few occasions in C-1, C-2, and C-4 was more abundant than *Moina*. *Ceriodaphnia* never was found in the treated ponds except in very small numbers in L-4, H-3, and H-4 on July 26 or August 7. *Diaphanosoma* appeared briefly in C-1 in late June and was never found elsewhere. On the last sampling date the control ponds averaged less than one cladoceran per 40 liters.

In high dose ponds each treatment was followed by a 99+% reduction of *Moina* populations, which made no or negligible recovery between treatments. In low dose ponds *Moina* populations declined by 99+% following the first treatment, but sometimes less following subsequent treatments. The July 1 treatment occasioned a decrease of only 84% in L-2, and the July 18 treatment a decrease of 30% in L-1 and a 170% increase in L-3. When *Moina* populations in treated ponds recovered, they often developed larger populations (e.g., L-2, L-3, H-2, and H-3) than were present at any time in the control ponds.

Data on the two copepods showed that (1) *Cyclops* populations developed more rapidly than those of *Diaptomus*, (2) *Cyclops* was more susceptible to Dursban than was *Diaptomus*, and (3) *Diaptomus* populations developed only when *Cyclops* was scarce or absent, either as a result of Dursban treatments or of other factors. At the beginning of the experiment

Cyclops was the dominant copepod in all ponds; *Diaptomus* was scarce in L-3, H-2, and H-3 and absent from the others. In control ponds *Cyclops* copepodids (= adults plus immature copepodids) fluctuated irregularly in abundance and were present only in very low numbers on the last sampling date (Fig. 5). *Diaptomus* copepodids were never found in C-1, C-2, or C-4, but in C-3 reached a maximum of 147 individuals per 40 liters on August 7.

In high dose ponds *Cyclops* copepodids were reduced in numbers by 97–99+% 24 hr after the first treatment. They never recovered in H-2 or H-3, but recovered well by early August in H-1 and H-4 (Fig. 5). In low dose ponds *Cyclops* copepodids were reduced by 60–98%, 89–99+, and 25–99+% at 24 hr after the first, second, and third treatments, respectively. Recovery of populations between treatments was good in L-1 and L-4 and moderate in L-2. In L-3 *Cyclops* completely disappeared after the second treatment and did not reappear until July 26. By the end of July *Cyclops* copepodids were as abundant or more abundant in L-1, L-2, and L-4 than they were in control ponds.

Diaptomus copepodids became more numerous in four of the treated ponds (L-1, L-3, H-2, and H-3) than they ever became in a control pond, and they also appeared in small numbers in two other treated ponds (L-2 and H-4) (Fig. 5). At the lower rate of

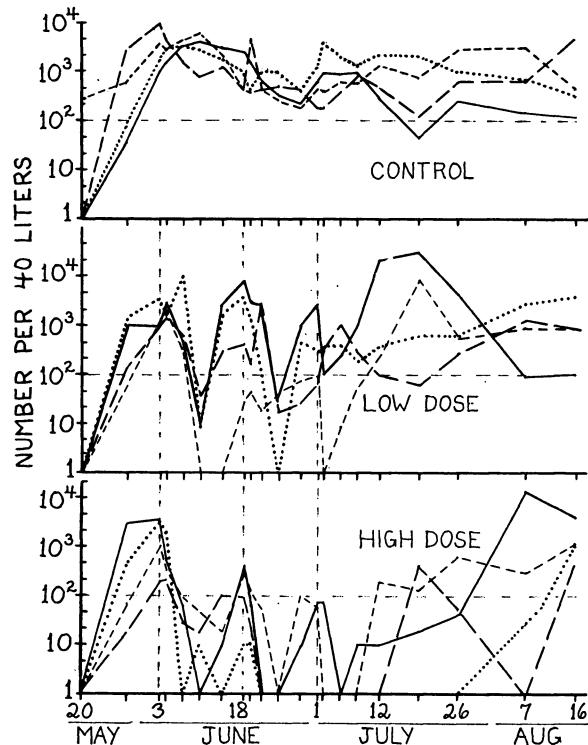


FIG. 6. Effect of insecticide treatment on the abundance ($n+1$) of copepod (*Cyclops* + *Diaptomus*) nauplii. Individual ponds represented as in Fig. 3.

application, Dursban appeared to have little or no acute toxicity for *Diaptomus*, which, 24 hr after treatment, had never declined by more than 10% of the pretreatment population. At the higher rate, 24 hr after treatment *Diaptomus* populations showed declines of 20% (H-2, second treatment), 3% (H-3, second treatment), and 91% (H-2, third treatment). *Diaptomus* populations remained small in high dose ponds until 2–3 weeks after the last treatment.

Dursban reduced the numbers of copepod nauplii, but this sometimes was not apparent until several days after treatment (Fig. 6). Perhaps nauplii tended to remain suspended in the water column for a short time following actual death. Although *Cyclops* and *Diaptomus* nauplii were not enumerated separately, the strong negative correlation between the abundances of these two species permitted the identity of the nauplii in a given pond on a given date. Evidence that *Diaptomus* nauplii were less susceptible to Dursban than *Cyclops* nauplii was provided by the low dose ponds following the third treatment. Where only *Diaptomus* was present (L-3), the number of nauplii had increased by 400% at 24 hr after treatment; where both were present (L-1), the number increased by only 11%; and where only *Cyclops* was present (L-2, L-4), the number decreased by more than 95%. On the last sampling date, nauplii, almost entirely *Diaptomus*, were 10–30 times more abundant in L-1, L-2, and L-3 than they were in L-4, where only *Cyclops* nauplii were present. In the high dose ponds almost all nauplii observed from June 10 to July 19 were *Diaptomus*; *Cyclops* nauplii did not reappear in any numbers until August and then only in H-1 and H-4.

Phytoplankton

Since the phytoplanktivorous crustaceans were temporarily eliminated by insecticide treatment, the increase in phytoplankton populations in the treated ponds was not surprising (Fig. 7). For control and treated ponds, geometric mean abundance of algal cells was high initially ($M_C = 70$, $M_L = 88$, $M_H = 57$, in millions per liter, May 20 or 28) and declined to a minimum ($M_C = 12$, $M_L = 33$, $M_H = 18$, in millions) on June 10. Thereafter, fluctuations of phytoplankton populations in control ponds were somewhat irregular although there was a tendency for increase, and maximum mean phytoplankton abundance occurred on August 16 ($M_C = 124$ million).

On June 4 and 7 the mean (geometric) number of algal cells was 30–38 million per liter for control and low and high dose ponds. By June 10 phytoplankton was significantly more abundant in low dose than in control ponds (Fig. 7); this initial difference was due to phytoplankton decreases in control ponds (from 33 to 12 million between June 7 and 10) and

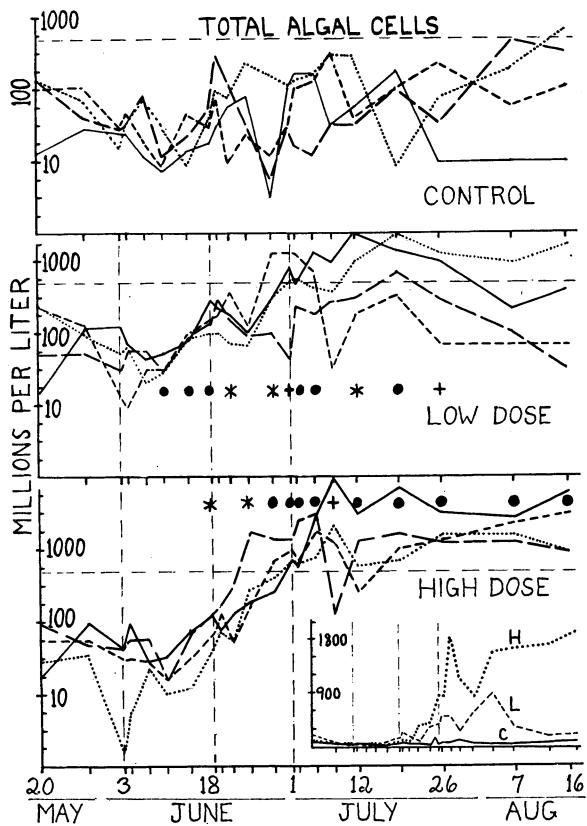


FIG. 7. Effect of insecticide treatment on the phytoplankton, expressed as total algal cells per liter. Individual ponds represented as in Fig. 3. Dashed horizontal reference line is drawn at 500 million cells per liter. Statistical significance determined by the Wilcoxon rank sum test and denoted as in Fig. 2. Inset shows geometric mean abundances plotted on an arithmetic scale.

the arrest of this natural decrease in low dose ponds ($M_L = 33$ million on both June 7 and 10). Subsequently, phytoplankton in low dose ponds increased to a maximum mean abundance of 910 million cells per liter on July 19 and then fell to 207 million on August 16.

Although crustaceans were completely eliminated in high dose ponds, the phytoplankton increases in these ponds lagged behind those in low dose ponds, at least initially. Phytoplankton was significantly more abundant in low dose than in the high dose ponds on June 14 ($M_L = 82$, $M_H = 37$, $P < 0.02$), June 18 ($M_L = 146$, $M_H = 79$, $P < 0.05$), and June 19 ($M_L = 180$, $M_H = 96$, $P < 0.10$). Previous to June 10, phytoplankton populations in low and high dose ponds were approximately the same, and after June 19 phytoplankton populations were always larger on the average in high dose ponds (Fig. 7). Phytoplankton populations in high dose ponds reached a maximum mean abundance of 1,942 million per liter on August 16, sixteenfold greater than the mean abundance of phytoplankton in control ponds on that date.

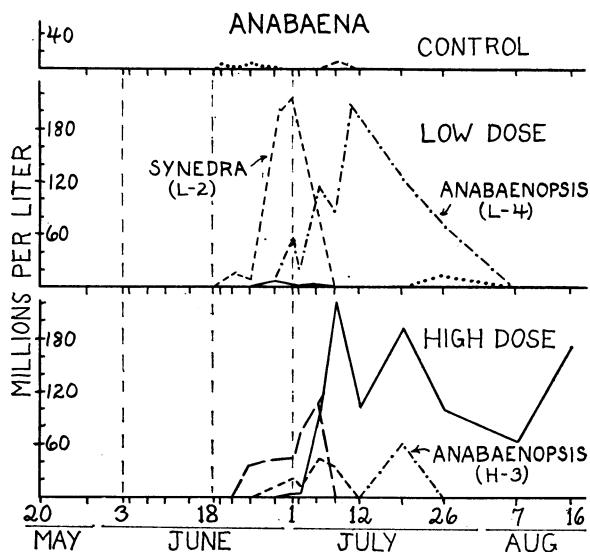


FIG. 8. Effect of insecticide treatment on diatom and filamentous bluegreen alga populations. Unless indicated otherwise, all lines represent *Anabaena* populations, and individual ponds are represented as in Fig. 3. For *Anabaena* and *Anabaenopsis* the ordinate measures millions of filaments per liter. Number of cells per filament taken as 100 for *Anabaena* and 10 for *Anabaenopsis* in calculation of total number of cells (Fig. 7). For *Synedra*, ordinate represents number of cells per 1/5.

Phytoplankton species varied considerably in their responses to insecticide treatments (Fig. 8 and 9). *Anabaena*, represented by at least three species, appeared in three of the control ponds and three of the low dose ponds, but only sporadically and always in low numbers. In three of the high dose ponds large *Anabaena* populations developed in late June and early July (Fig. 8) and covered portions of these ponds with a powdery green scum for 1 or more weeks. During this time *Anabaena* was the dominant alga in these ponds, and when it declined during the second week in July there was a temporary decline in total phytoplankton (Fig. 7). Subsequently other algal populations, primarily of unicellular species, increased to return phytoplankton populations in high dose ponds to their former high level.

Anabaenopsis was not observed in any ponds other than L-4 and H-3, but in these it appeared in bloom proportions, the bloom lasting for more than a month in L-4 (Fig. 8).

Diatoms generally were more abundant in low dose ponds. In neither a control nor a high dose pond did the number of diatoms ever exceed 10 million per liter. Yet they exceeded this level once in L-1, nine times in L-2, once in L-3, and seven times in L-4. In L-2 a small species of *Synedra* (length = 25 μ , maximum width = 2 μ) increased after the second treatment, attained a density of more than one billion cells per liter by July 1, and declined rapidly thereafter (Fig. 8).

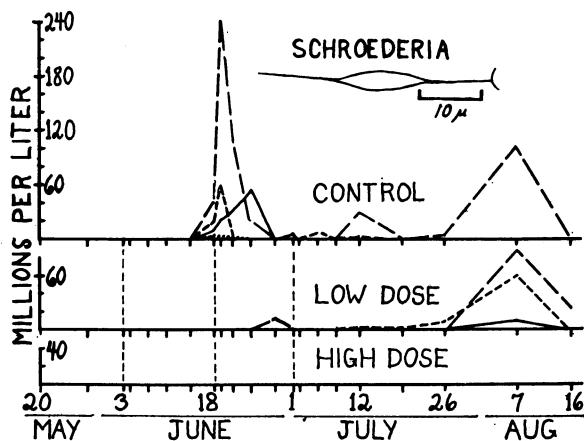


FIG. 9. Effect of insecticide treatment on the alga *Schroederia setigera* (Characiaceae: Chlorophyta). Individual ponds represented as in Fig. 3.

The effect of insecticide treatment on populations of the delicate, spined *Schroederia setigera* (length = 30–40 μ) was essentially the reverse of its effect on total phytoplankton. *Schroederia* was continuously present in all four control ponds during the second half of June and became exceptionally abundant in three of them (Fig. 9). These *Schroederia* populations were the primary cause of the increase in total phytoplankton in control ponds from a mean of 12 million cells per liter on June 10 to a mean of 85 million cells per liter on June 19. *Schroederia* was found sporadically in C-2, C-3, and C-4 throughout the rest of the experiment, becoming quite abundant in C-3 on two occasions. It was never found in the high dose ponds or in L-1, but was present in moderate numbers (1.1 million cells per liter) in L-3 on June 28 and in moderate to large numbers in L-2, L-3, and L-4 on August 7.

Examination of the zooplankton samples provided qualitative information on *Euglena*, *Pediastrum*, and *Ulothrix* populations. *Euglena* was never common in the control ponds. In L-4 a very large population of *Euglena* developed immediately following the first treatment and persisted through June and July; throughout this period the surface of L-4 was covered with a yellow-green film consisting almost entirely of *Euglena*. *Euglena* became briefly abundant in three of the high dose ponds during the first week of July, but not as abundant as in pond L-4.

Cottony, diffuse yellowish masses of a *Ulothrix* (?) species (cell length = 25–50 μ , width = 4.5 μ) were very abundant in C-3 from mid-June to July 12 and in L-2 on August 7 and 16. They were suspended in the lower half of the water column and were not at all represented in the phytoplankton samples. They greatly reduced the efficiency with which the plankton net collected zooplankters on those dates.

Pediastrum appeared in some abundance in one

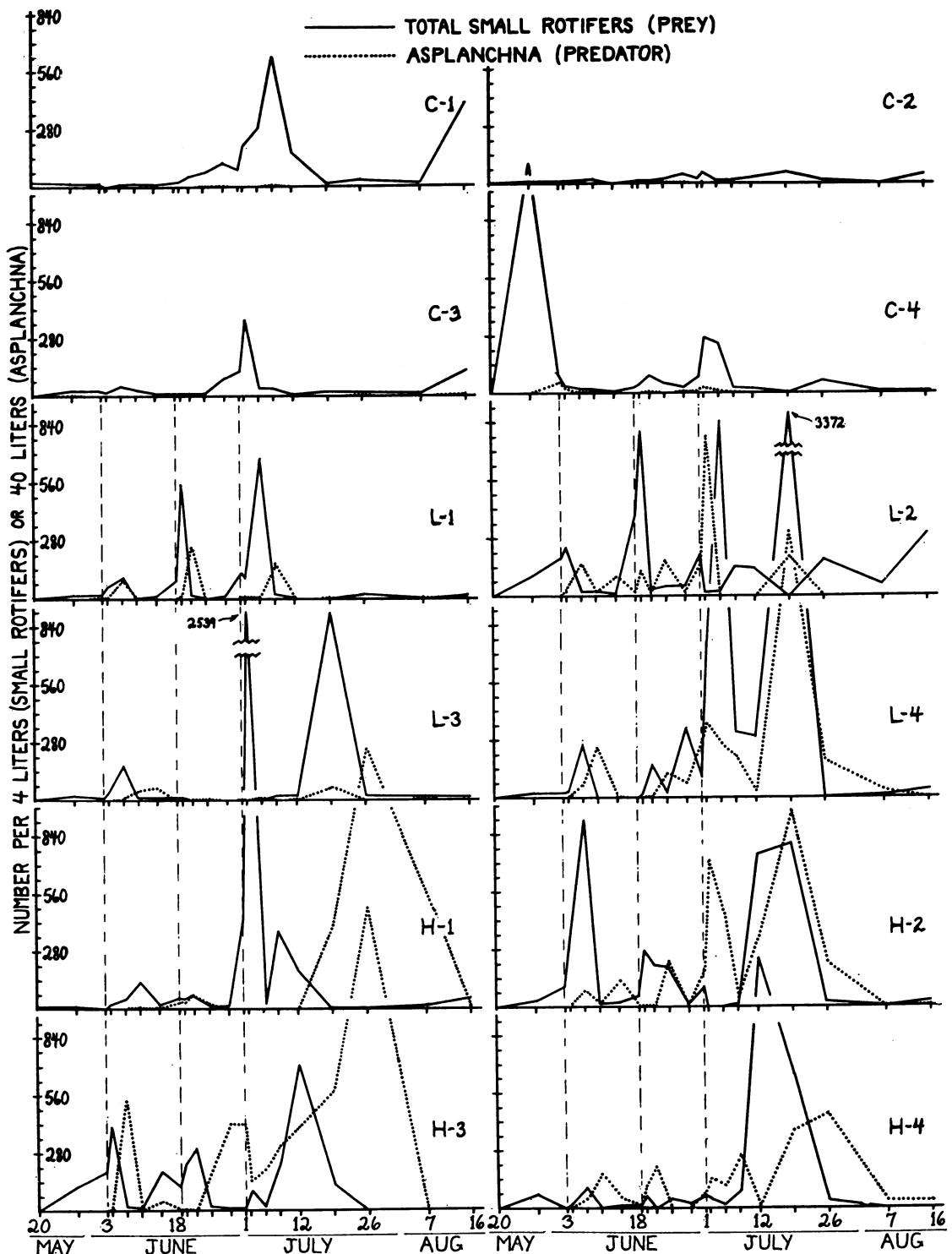


FIG. 10. Effect of insecticide treatment on the predaceous rotifer *Asplanchna brightwelli* and on the small rotifer populations.

control (C-1), two low dose ponds (L-2 and L-4), and three high dose ponds (H-1, H-2, and H-3) sometime between the middle of July and early August.

Although it is not planktonic, the exceptional development of the filamentous alga *Cladophora* sp. in C-4 must be noted here. Mats of this alga began forming on the bottom of C-4 in mid-July, and by August 16 they so completely clogged the pond that use of a plankton net was impossible and zooplankton samples had to be collected by dipping into the remaining spots of open water with a bucket. This development of *Cladophora* appeared to have a negative effect on the phytoplankton and bacteria as both were extremely scarce in C-4 on July 26 and August 7 and 16 (Fig. 7).

Small rotifers

Rotifer population explosions, involving not only the predaceous *Asplanchna brightwelli* Gosse, as observed in our earlier study (Hurlbert et al. 1970), but also at least six other rotifer genera, occurred

after almost every insecticide treatment (Fig. 10). *Asplanchna* populations usually increased only after small rotifers (i.e., all rotifers except *Asplanchna*) became abundant, and, in general, large populations of small rotifers developed only when crustacean, especially cladoceran, populations were small. This latter relationship is readily seen in a pond comparison of Fig. 5 and 10. Rotifers and cladocerans were rarely simultaneously abundant, although they frequently were simultaneously scarce (Fig. 11). The few occasions on which rotifers and cladocerans coexisted in moderate numbers were either when phytoplankton populations were rapidly increasing (e.g., *Filinia* and *Hexarthra* in treated ponds) or when the dominant rotifers were benthic-littoral types (e.g. *Lecane*, *Euchlanis*, and *Monostyla* in control ponds) that may not have been in such strong competition with *Moina* and *Ceriodaphnia* as were more planktonic rotifers.

A negative relation between rotifer and crustacean abundances was first apparent 10 days after the ponds were flooded. On May 28, of the control ponds, C-4

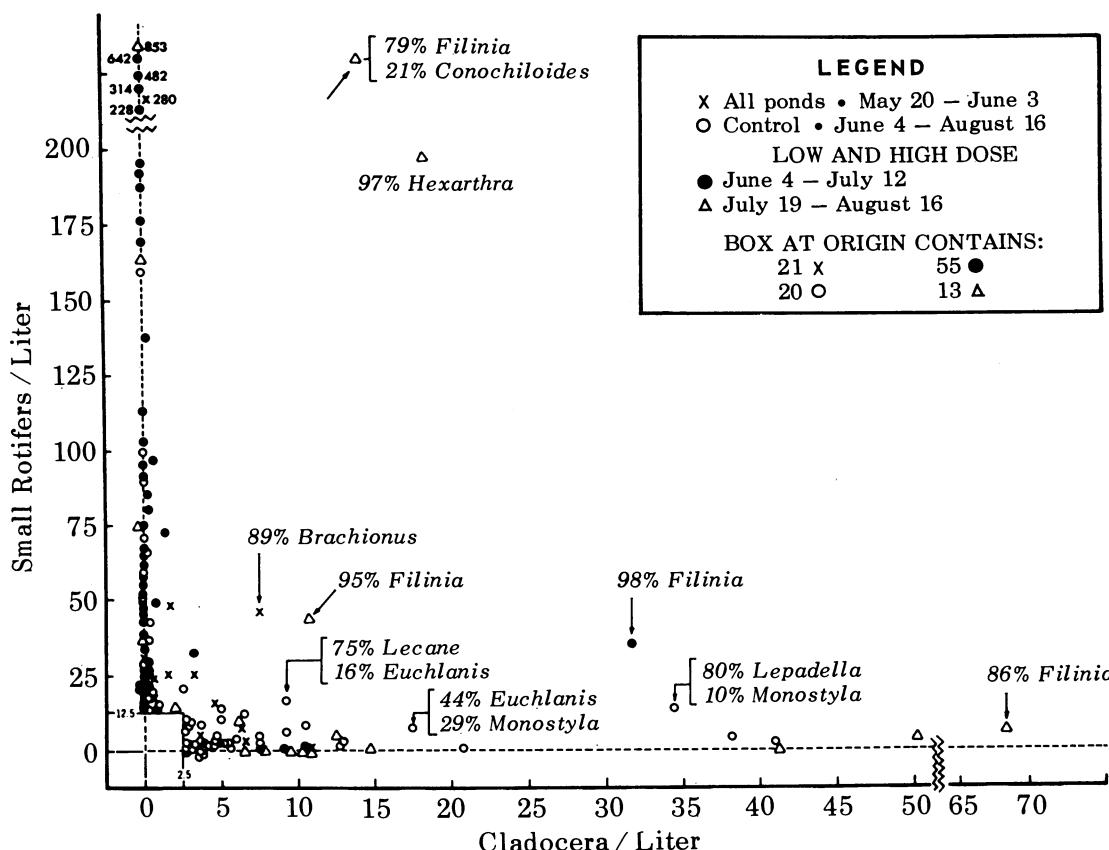


FIG. 11. The negative correlation between the abundances of small rotifers and Cladocera. Of 252 points (12 ponds, 21 dates), 109 which would have fallen in the box at the origin have not been plotted. The observed proportion (4%) of samples where both rotifers and cladocerans were "abundant" (rotifers > 12.5/liter, cladocerans > 2.5/liter) was significantly ($P < 0.01$) less than the proportion (9%) expected on the assumption of independence (chi-squared test of 2 x 2 contingency table). For certain samples the dominant rotifers have been indicated.

TABLE 1. Statistical summary of the abundance of rotifers on the 18 sampling dates after the first insecticide treatment. C = control ponds; L = low dose ponds; H = high dose ponds. Although means are reported separately for high and low dose ponds, the statistical significance of the effect of treatment was determined by grouping all eight treated ponds together and comparing them with the control ponds by the Wilcoxon rank sum test (Wilcoxon and Wilcox 1964). Significance levels denoted as in Fig. 2. Numbers and symbols in parentheses show the effect of eliminating the data for C-3 from the statistical analyses

Rotifer species	Geometric mean abundance ^a			Effect (%) ^b of treatment	P	Three largest populations ^c (after June 3)	
	C	L	H			Number/11 liters	Corresponding ponds
Species with small toes or with foot completely lacking—presumably planktonic							
<i>Asplanchna brightwelli</i>	0.4	7.6	23.0	+3500	**	1,469, 1,287, 1,267	H-3, L-4, H-1
<i>Brachionus</i> spp.	3.4	18.6	21.3	+485	*	9,635, 6,865, 2,309	L-4, H-1, L-2
<i>B. angularis</i>	0.7	3.9	4.5	+500	ns	6,247, 2,166, 1,790	H-1, L-2, L-1
<i>B. quadridentata</i>	0.7	0.9	1.0	+31	ns	147, 130, 85	C-1, L-4, H-1
<i>B. budapestinensis</i>	0.4	1.0	5.5	+800	ns	1,108, 1,056, 1,055	H-2, C-1, H-1
<i>B. urceolaris</i>	0.4	0.5	0.8	+72	ns	129, 92, 59	C-3, C-1, H-1
<i>B. bidentata</i>	0.3	1.6	0.2	+150	ns	9,635, 105, 40	L-4, C-3, L-3
<i>B. plicatilis</i>	0.03	0.04	0.04	+33	ns	3, 2	C-3, H-1
<i>B. calyciflorus</i>	0.00	0.07	0.06	+∞	+	25, 17, 3	L-4, H-2, H-1
<i>Polyarthra trigla</i>	8.1	4.3	4.9	-43	ns	557, 530, 522	C-1, H-2, C-4
<i>Hexarthra intermedia</i>	2.2	1.9	3.8	+25	ns	3,810, 3,460, 2,170	L-4, H-4, H-2
<i>Filinia terminalis</i>	0.1	2.7	0.9	+1540	**	2,000, 463, 104	L-3, L-2, H-2
<i>Epiphantes brachionus</i>	0.00	0.02	0.03	+∞	+	132, 83, 9	H-1, H-4, H-3
<i>Keratella</i> spp.	0.1	0.02	0.02	-80	ns	69	C-3
Species with well-developed toes—presumably benthic or littoral, or both							
<i>Lecane</i> spp.	3.3 (5.5)	0.7	0.2	-86 (-92)	ns (**)	151, 144, 109	L-4, C-1, C-4
<i>Monostyla</i> spp.	3.3 (5.7)	0.2	0.6	-87 (-92)	+(**) 1,000, 56, 50	C-1, C-4, C-2	
<i>M. quadridentata</i>	2.6 (4.3)	0.06	0.4	-91 (-95)	* (**) 593, 55, 49	C-1, C-4, C-2	
<i>Platyias quadricornis</i>	0.3 (0.5)	0.03	0.03	-90 (-94)	+(**) 19, 4	C-1, L-2	
<i>Lepadella</i> sp.	0.2 (0.3)	0.00	0.07	-80 (-87)	ns (**) 116, 23, 2	C-2, C-1, H-1	
<i>Testudinella patina</i>	0.2 (0.2)	0.08	0.01	-80 (-80)	* (**) 17, 5, 5	L-4, C-1, C-3	
<i>Tripleuchlanis plicata</i>							
+ <i>Euchlanis dilatata</i>	1.8 (2.4)	0.9	0.6	-58 (-68)	ns (*)	1,290, 72, 35	L-4, H-1, C-2

^aCalculated as antilog $\left[\sum_{i=1}^4 \sum_{j=4}^{21} \log_{10} (N_{ij} + 1)/(4) (18) \right] - 1$, where N_{ij} is the number of individuals counted in 11 liters of water (or 40 liters in the case of *Asplanchna*) from the i^{th} pond (in a set of 4) on the j^{th} sampling date.

^bCalculated as $(M_{L,H} - M_C)/M_C$ where M_C is as given in the column headed C and $M_{L,H}$ is the geometric mean abundance calculated over all eight treated ponds, this being slightly different from the mean of columns L and H.

^cNo pond permitted to be listed twice. Fewer than three populations listed indicates that fewer than three ponds had maxima greater than one individual per 11 liters.

had the most rotifers, but the fewest *Cyclops* nauplii and copepodids and the second fewest *Moina*; of the low dose ponds, L-2 had the most rotifers, but the fewest *Cyclops* nauplii and copepodids and the fewest *Moina*; of the high dose ponds, H-3 had the most rotifers, but the fewest *Cyclops* nauplii and copepodids and the fewest *Moina*. After May 28 there was no clear relation between the abundances of *Cyclops* and the small rotifers.

In control ponds large posttreatment rotifer populations were present only during the brief period in early July when cladocerans were rare or absent, and on August 16, by which time the cladocerans had disappeared again (Fig. 5 and 10). In treated ponds rotifer populations usually increased markedly, often five- to twentyfold, within 1–3 days after treatment. Physiologically, these increases were permitted by water temperatures frequently in excess of 30°C, for even at 20°C, rotifers of genera such as *Brachionus*, *Polyarthra*, and *Asplanchna* have generation times (egg to production of first egg) of only 40–52 hr (Pourriot and Hillbricht-Ilkowska 1969).

Such population increases were inhibited if large numbers of Dursban-tolerant *Diaptomus* (e.g., L-3, second and third treatments) or *Asplanchna* (e.g., L-2, H-2, H-3, and H-4, third treatment; but cf. L-4, third treatment) were present at the time of treatment. In some instances treatment came at a time when the populations of small rotifers already were increasing rapidly (e.g., L-2, second treatment; L-3, third treatment). On these occasions the posttreatment increases in rotifer numbers may have occurred despite, not because of, the insecticide treatment.

The species of rotifers found in the ponds are listed in Table 1 and several are illustrated in Fig. 12. Insecticide treatment generally had either no effect or a positive one on the occurrence and abundance of planktonic rotifers, but it had a negative effect on the abundance of benthic-littoral species (Table 1). The division of the species into planktonic and benthic-littoral types was based on foot morphology, which, in the opinion of most authorities, relates closely to habitat. A foot is completely absent in *Asplanchna*, *Polyarthra*, *Hexarthra*, and

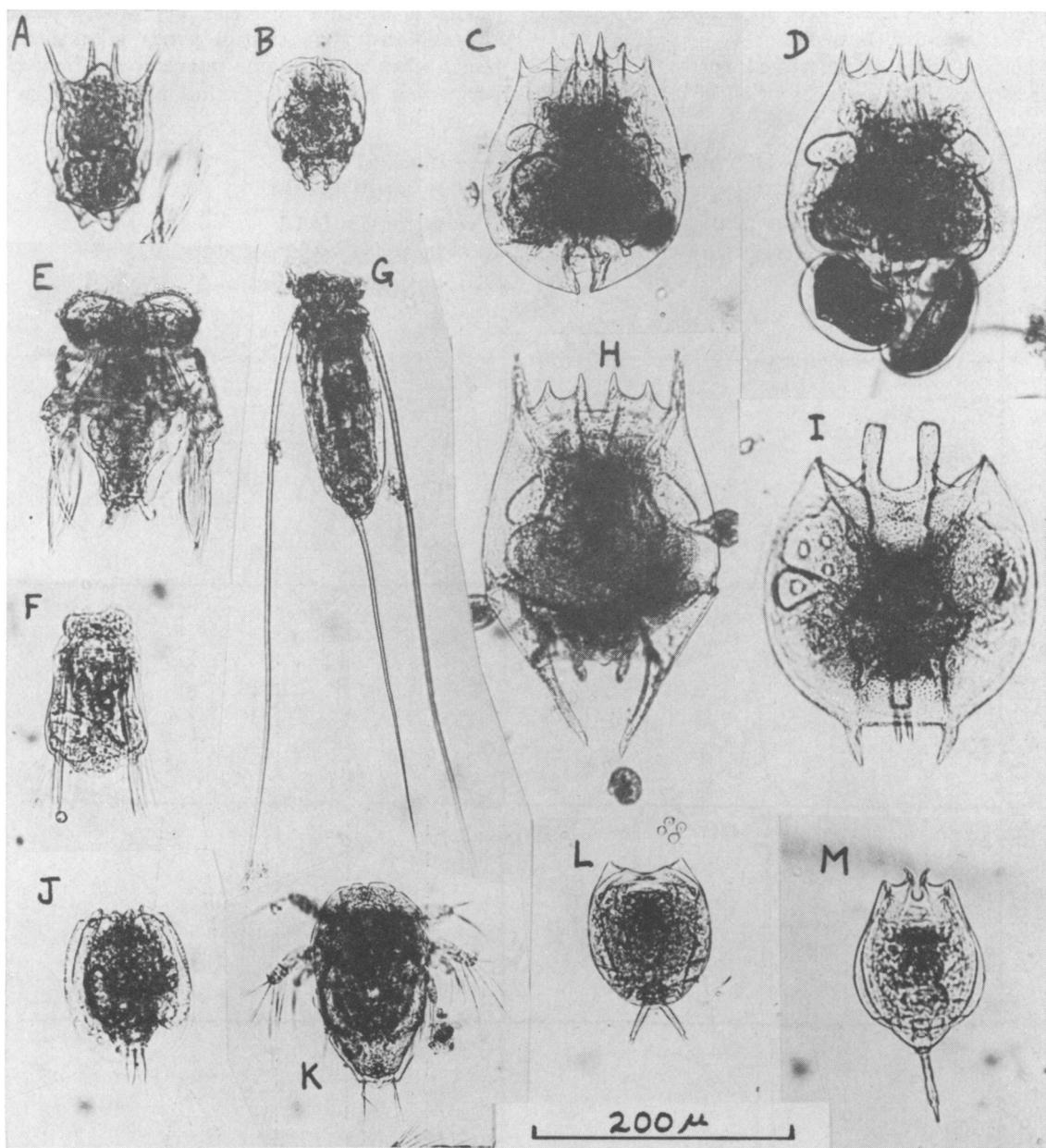


FIG. 12. Some of the common rotifers in the experimental ponds and (K) a *Cyclops vernalis* nauplius, for comparison. A, *Brachionus budapestinensis*; B, *B. angularis*; C, *B. ureceolaris*; D, *B. quadridentata*; E, *Hexarthra intermedia*; F, *Polyarthra trigla*; G, *Filinia terminalis*; J, *Tripleuchlanis plicata*; L, *Lecane luna*; M, *Monostyla quadridentata*.

Filinia. In *Brachionus*, *Epiphantes*, and *Keratella* a foot is present, but is equipped with very small toes. In *Monostyla*, *Lecane*, *Platyias*, *Triplanchlanis*, *Euchlanis*, and *Lepadella* a foot is present and is equipped with moderately to well-developed toes; these have the form of one or two stout movable spines and usually are visible even when the foot is retracted (Fig. 12-I, J, L, M). According to Pennak (1953:164), "Most of the free-swimming, non-plankton species having a foot and toes are able to

creep about and browse on substrates as a result of the beating of the coronal cilia against the substrate combined with a pushing action of the toes." Edmondson (1959:425) states that "in general, the foot is small or absent in planktonic rotifers," and Hyman (1951:41) offers a similar opinion. *Testudinella* is somewhat exceptional in possessing a well-developed foot but no toes; however, it is "found in ponds among vegetation" (Hyman 1951:125) and is referred to as "heleoplanktonic and littoral-benthic"

by Hutchinson (1967:518), so we have grouped it with the large-toed forms.

The combining of all treated ponds for the purpose of calculating an index of effect in Table 1 was

justified in that low dose and high dose ponds generally differed from control ponds in qualitatively similar ways as far as the population of any given species was concerned. Exclusion of the data for

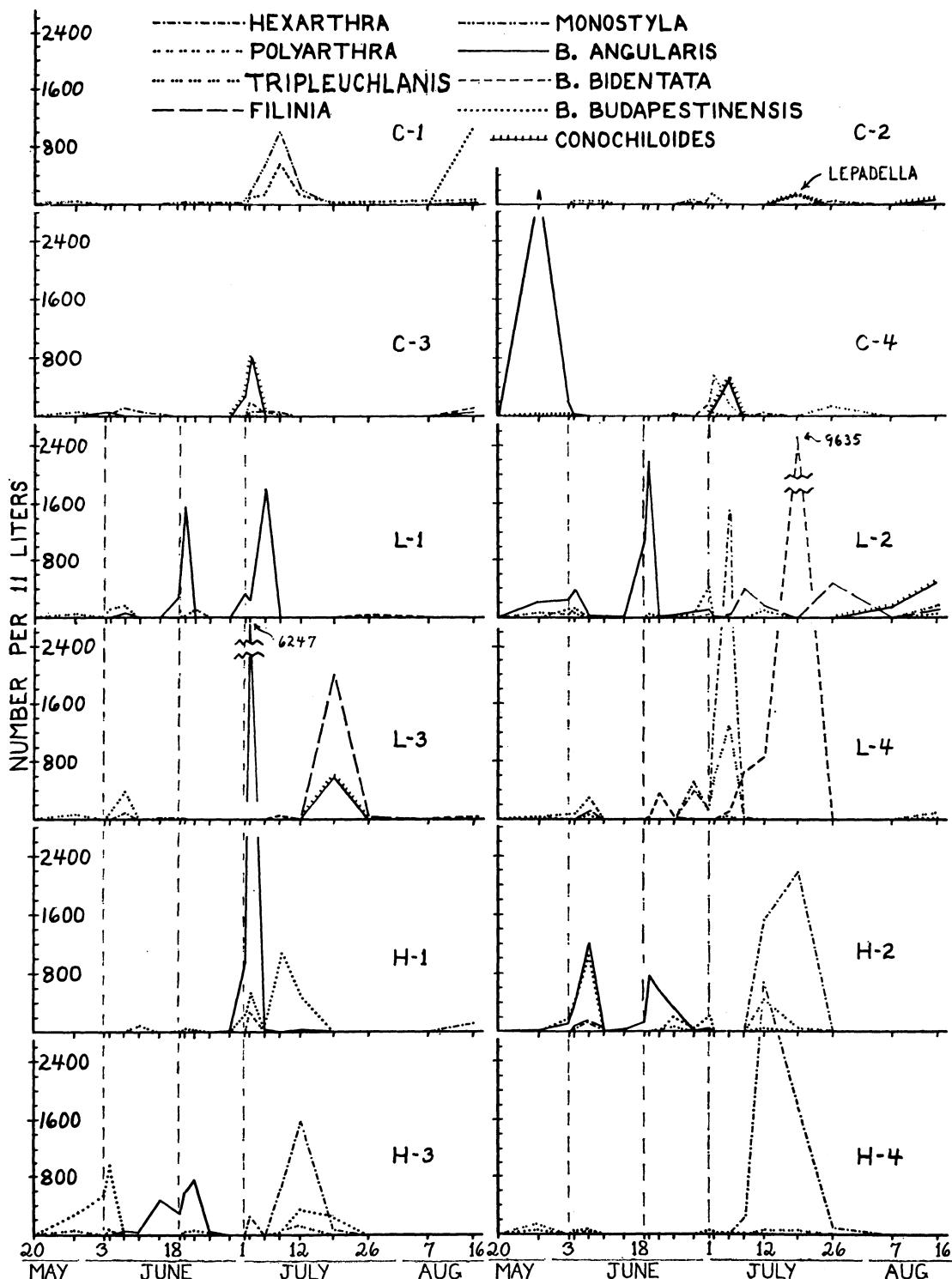


FIG. 13. The effect of insecticide treatment on the various species of small rotifers.

C-3 from analysis increased the magnitude and statistical significance of the effect of treatment on the benthic-littoral species. Although invalid in principle, the effect of this exclusion seemed worth demonstrating since every benthic-littoral species or genus listed in Table 1 was both less abundant and less frequent in C-3 than in any of the other control ponds. The bottom of pond C-3 was covered with extensive masses of a delicate *Ulothrix* for a month during the middle of the experiment.

Considered individually, the small rotifer species showed a variety of responses to treatments and correlations with other populations. Of all of them, *Filinia terminalis* (Plate) was affected most favorably by insecticide treatments. Although rarely a dominant, the ratio of its mean abundance in treated versus control ponds was higher than that for any other herbivorous rotifer, possibly because it was less affected by the 35-fold increase in *Asplanchna* populations (Fig. 13, Table 1). The setae of *Filinia* (Fig. 12-G) permit it to jump or somersault rapidly aside when it bumps into another organism or object and undoubtedly function as a mechanism of escape from predators such as *Asplanchna*. Pourriot (1964) showed that the presence of a substance secreted by *Asplanchna* causes a marked elongation of the setae of *Filinia mystacina*.

Filinia was found in only four of the 72 control-pond samples taken after June 3. In both low and high dose ponds it appeared sporadically in low numbers (maximum = 104/11 liters) throughout June. Thereafter *Filinia* was essentially absent from high dose ponds, but persisted in low dose ponds, reaching maximum abundance in L-1, L-2, and L-3 sometime between July 19 and August 16. *Filinia* was rare throughout the entire experiment in L-4, where *Euglena* was so abundant.

Brachionus was represented by no less than seven species in the experimental ponds (Table 1). *Brachionus plicatilis* O. F. Müller and *B. calyciflorus* Pallus were never more than rare, and the former never occurred in a control pond although it did appear in five of the eight treated ponds. In general, the genus was poorly represented in control ponds except for the brief development of *B. budapestinensis* Daday in C-1 (August 16) and of *B. angularis* Gosse in C-4 (May 28).

Comparison of the five most abundant species of *Brachionus* (Fig. 10, 12, and 13; Table 1) showed that the smallest species, *B. angularis* and *B. budapestinensis*, profited most from insecticide treatment. *Brachionus angularis* often showed the largest population increase immediately after treatment. It achieved its greatest abundance in H-1 when *Asplanchna* appeared to be completely absent (Fig. 10 and 13). *Brachionus budapestinensis*, with a few exceptions, was rare in control and low dose ponds,

but in each high dose pond except H-3 it developed large populations on several dates. Its peaks of abundance usually followed and were smaller than those of *B. angularis*. Increases in the ratio of *B. budapestinensis* to *B. angularis* were frequently associated with high *Asplanchna* populations (e.g., L-2, H-2, H-3) and no doubt were fostered by *Asplanchna*'s preference for *B. angularis* (Table 3). However, in H-1 *B. budapestinensis* replaced *B. angularis* even in the absence of *Asplanchna*. Its slightly larger size may permit *B. budapestinensis* to feed on a wider size range of phytoplankters than *B. angularis* can, thereby giving the former a competitive advantage under stable conditions. *Brachionus angularis* cannot utilize *Phacus pyrum* because this alga is too large, but five larger species of *Brachionus* thrive on it, and all six species can use the small *Chlorella* (Pourriot 1965b).

The three larger species, *B. urceolaris*, *B. quadridentata*, and *B. bidentata*, were as abundant in control ponds as *B. angularis* and *B. budapestinensis*, but responded slowly and generally undramatically to insecticide treatment (Table 1), perhaps because of their longer generation times. *Brachionus urceolaris* was very rare in control ponds during June, but sporadically appeared in small numbers in six of the treated ponds following the first treatment; in July it became less frequent in treated ponds and more frequent in control ponds. *Brachionus quadridentata* was present in small numbers in all ponds before the first treatment, became even rarer during June in control ponds, but increased slightly in five or six treated ponds soon after the first treatment; it was rare in all ponds after June 18. *Brachionus bidentata* was generally rare in all ponds except in L-3, where it developed a small but persistent population subsequent to the third treatment, and in L-4, where it became more abundant than any other rotifer during the experiment. This exceptional development in L-4 required the better part of 2 weeks and was apparently related to the rich supply of *Euglena* there. Also, the large size and spines of *B. bidentata* were probable deterrents to predation by *Asplanchna* and, possibly, *Cyclops*, both of which were abundant in L-4 (Fig. 5, 10). Very effective deterrence of *Asplanchna* has been demonstrated for the similar spines of *B. calyciflorus* (Gilbert 1967).

Hexarthra intermedia Wiszniewski, the dominant if not only representative of this genus in the ponds, appeared in greatest numbers during or immediately following the *Anabaena* and *Anabaenopsis* blooms in L-4, H-2, H-3, and H-4 (Fig. 8, 13). We occasionally observed cells and short filaments of *Anabaena* in *Hexarthra* stomachs. In H-1, where neither *Anabaena* nor *Anabaenopsis* populations developed, *Hexarthra* was essentially absent until August 16. Throughout the experiment *Hexarthra* was mostly

absent from C-1, C-2, L-1, and L-2 and persisted in small numbers in C-3, C-4, and L-3.

On the basis of its geometric mean abundance, *Polyarthra trigla* Ehrenberg was the most successful herbivorous rotifer in both control and treated ponds, yet its maximum recorded abundance was less than the maximum recorded abundances of at least nine other species (Table 1). In addition, it was the only planktonic rotifer that was less abundant in treated than control ponds. After the initial flooding of the ponds, *Polyarthra* populations developed more rapidly than those of any other rotifer. It was absent in all ponds on May 20, but on May 28 had a geometric mean abundance of 28 individuals per 11 liters; the next most rapidly appearing rotifer, *Brachionus angularis*, had a mean abundance of only eight individuals on May 28. In control ponds *Polyarthra* persisted in low numbers until the end of June, reached peak abundances in early July, and declined thereafter. In low dose ponds *Polyarthra* peaked within a week after the first treatment and then declined to low numbers for the remainder of the experiment, with the exception of brief peaks in L-1 (July 5) and L-2 (August 16). In high dose ponds, *Polyarthra* populations exhibited low maxima during the week following the first treatment, declined during the remainder of June, and peaked again and at higher levels following the third treatment.

Polyarthra showed a clear negative correlation with *Diaptomus* populations. It disappeared ($n \leq 1/11$ liters) from C-3, L-1, and L-3 after *Diaptomus* populations in these ponds exceeded 100 individuals per 40 liters. It likewise disappeared when *Diaptomus* began increasing in H-2 and H-3, but in these ponds *Asplanchna* increased at the same time and preyed on *Polyarthra*. In all other ponds *Diaptomus* was scarce or absent and *Polyarthra* populations fluctuated at low levels, rarely disappearing except when *Asplanchna* was abundant.

Although rare, the remaining planktonic rotifers did show some consistent trends. *Epiphantes brachionus* (Ehrenberg) was never observed in control ponds and was found on one occasion in L-2 and on one to three occasions in each of the high dose ponds. The illorate rotifer *Conochiloides dossuarius* (Hudson) is not listed in Table 1 because it contracted into an unrecognizable form when preserved and therefore usually was not identified except when abundant. Heating for a few minutes in a 5% potassium hydroxide solution cleared and expanded this rotifer, permitting its identification. *Conochiloides* was observed in three of the control ponds and in one low dose pond, but was not observed in the high dose ponds. It tended to be the dominant rotifer when *Ulothrix* was present (Fig. 13; C-3, L-2). *Keratella cochlearis* and *K. gracilenta* were both too rare for any trends to be discerned.

Although each benthic-littoral rotifer was more abundant in the control than in the treated ponds, three of them, *Lecane* spp., *Tripleuchlanis plicata* Levander, and *Testudinella patina* (Hermann), had their best development in L-4 during the *Euglena* bloom in early July (Table 1). In their respective treatment levels, benthic-littoral rotifer populations were largest and most persistent in ponds C-1 and H-1; these two ponds had not been filled the previous year.

Lecane, represented primarily by *L. luna* O. F. Müller (Fig. 12-L), was absent or rare in all ponds up through June 14. Small to moderately large populations developed in late June and early July in C-1, C-2, C-4, and L-4; otherwise, *Lecane* was rare. *Monostyla*, represented primarily by *M. quadridentata* Ehrenberg, exhibited a similar pattern of occurrence, except that it was rare in L-4 and better represented in H-1. *Platyias quadricornis* Wizniewski, *Testudinella patina*, and *Lepadella* sp. were almost always rare, but were present more often in samples from control than from treated ponds.

Euchlanis dilatata Ehrenberg and *Tripleuchlanis plicata* were not distinguished from each other in the original analysis of samples. Subsequent examination of those samples in which they were moderately to very abundant showed that *Euchlanis* was the less abundant of the two in the control ponds and rare if not absent in the treated ponds. Collectively, the two species persisted in small numbers in C-1, C-2, and C-4 from June 10 to the end of July, but were very rare in C-3. They appeared in each low dose pond for 4-7 days after the first treatment and then disappeared for the rest of the experiment, except in L-4 (Fig. 13). A small population of *Tripleuchlanis* appeared in H-1 and in H-4; otherwise, these rotifers were rare.

Asplanchna

Asplanchna brightwelli was rare or absent in all control ponds throughout the experiment, never exceeding 50 individuals per 40 liters (C-4, June 3). Its dramatic fluctuations in the treated ponds are shown in Fig. 10. *Asplanchna* feeds primarily on small rotifers, and when these increased following treatment, *Asplanchna* increased also. There were few exceptions: *Asplanchna* seemingly failed to respond to the large *B. angularis* population developing in H-1 after the third treatment, and in both H-1 and H-3 peak *Asplanchna* populations were delayed, appearing 2 or more weeks after the peak abundance of herbivorous rotifers. There was no indication that Dursban, at either the low or high dose, was toxic to *Asplanchna*.

Asplanchna exhibited much intra- and interpopulational variation in body size and shape (Fig. 14), in size of trophi or jaws (Fig. 15), and in correlated

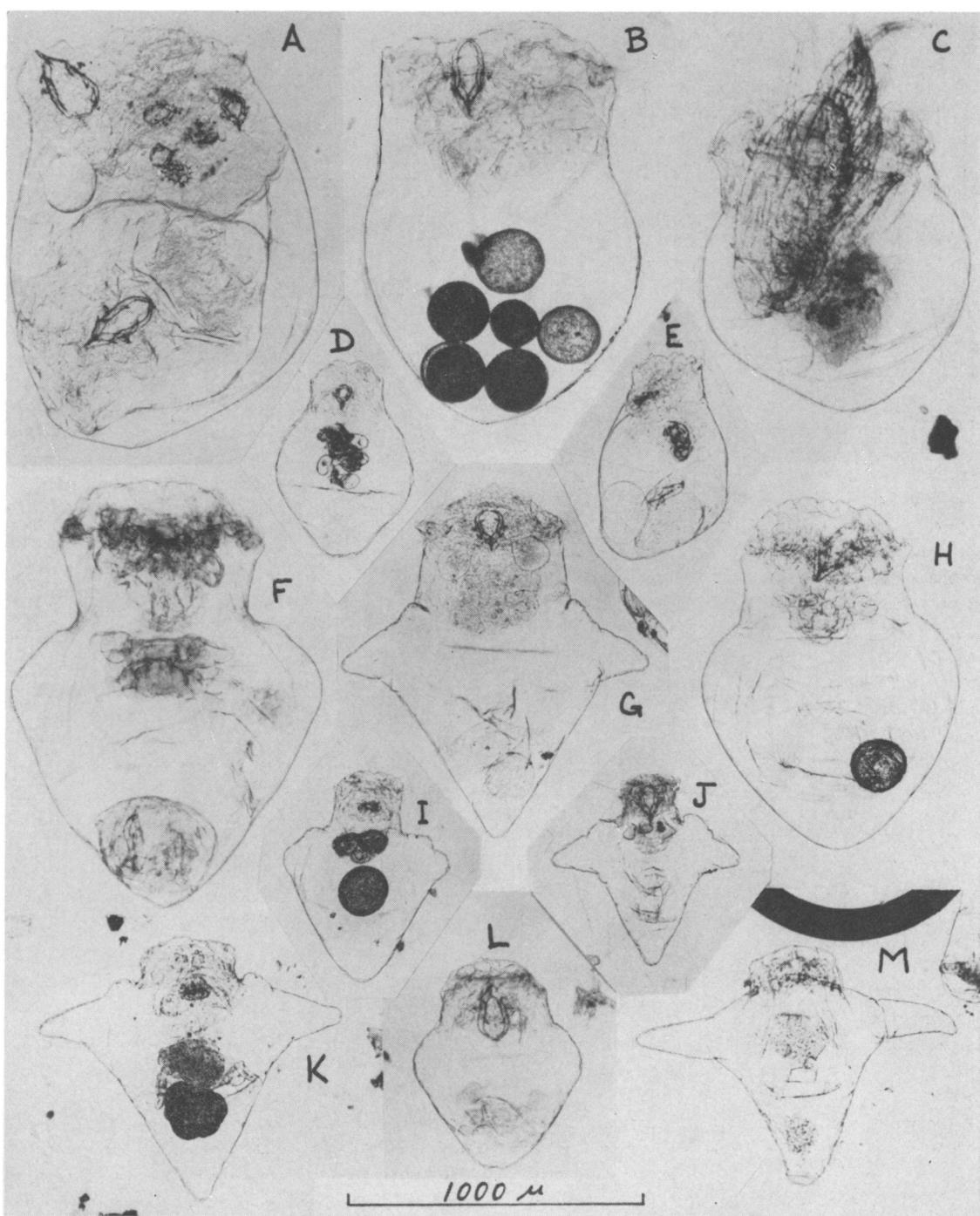


FIG. 14. Morphotypes of *Asplanchna brightwelli* found in insecticide-treated ponds. l = length, w = maximum width, t = length of ramus of trophi (i.e., straight-line distance from tip of ramus to its articulation with the fulcrum); all measurements in microns (μ). Camp. = campanuliform morphotype, ampull. = ampulliform morphotype, cruc. = cruciform morphotype. A, camp. ($l = 1,300$, $t = 250$), lateral view, with embryo ($l = 900$, $t = 250$) in uterus and with trophi ($t = 120$, 120 , 100) of three cannibalized *Asplanchna* in its stomach, along with a *Pediastrum coenobium*. B, camp. ($l = 1,200$, $t = 240$) with six resting eggs in uterus. C, camp. ($l = 1,000$, $t = 260$) ingesting *Diaptomus pallidus* (l , excl. setae = $1,100$). D, ampull. ($l = 600$, $t = 80$) with loricas and eggs of *Brachionus angularis* in stomach. E, ampull. ($l = 600$, $t = 90$), lateral view, with loricas of *Brachionus angularis* in stomach and with embryo ($t = 140$) in uterus. F, cruc. ($l = 1,300$, $t = 120$) with embryo ($t = 200$) in uterus. G, cruc. ($l = 1,100$, $t = 120$) with small embryo in uterus. H, camp. ($l = 1,100$, $t = 230$) with resting egg in uterus. I, cruc. ($l = 700$, $t = 110$) with loricas of *Brachionus angularis* in stomach and one resting egg in uterus. J, cruc. ($l = 650$, $t = 100$). K, cruc. ($l = 850$, $t = 100$) with resting egg being formed. L, camp. ? ($l = 700$, $t = 190$). M, male ($l = 900$, $w = 1,100$), viewed slightly obliquely from above, with testis visible in posterior end of body.

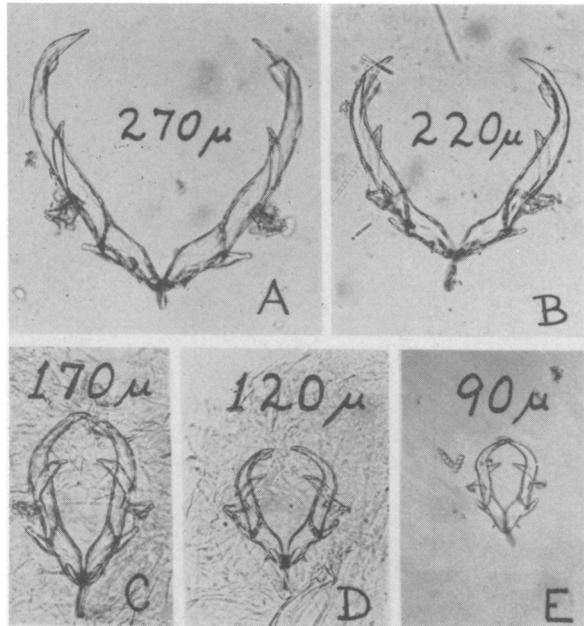


FIG. 15. Variation in the size of trophi of *Asplanchna brightwelli* from insecticide-treated ponds. Measurement given is the straight-line distance from the distal tip of a ramus to its articulation with the fulcrum.

ecological properties such as diet, propensity for cannibalism, and the production of resting eggs (Table 2). Most females were readily assigned to one of the three basic morphotypes described by Powers (1912): ampulliform (Fig. 14-D, E), cruciform (Fig. 14-G, J, K), or campanuliform (Fig. 14-A, B), to employ the very descriptive terminology of Beauchamp (1951).

The first individuals to appear in a pond were invariably ampulliforms measuring 400–650 μ long and with trophi 80–90 μ long (Fig. 14-D, E, Fig. 15-E). In general, whenever a population rose from near zero to a large size in a period of 1–3 days, ampulliforms were the dominant morphotype. Ampulliforms had several reproductive options. On rare occasions they were found to contain resting eggs, although never more than one egg per individual (Table 2: L-2, July 2, 19; L-4, July 2). (The few campanuliforms present on these occasions possessed no resting eggs.) Parthenogenetically, ampulliforms were able to give rise to cruciforms, to other ampulliforms either the same size or larger, and to campanuliforms. Sometimes as many as nine embryos were present in a single small ampulliform. Transformation to a well-developed cruciform morphotype (Fig. 14-K) appeared to require two or more generations, intermediate generations having intermediate morphologies (e.g., Fig. 14-I). For the purposes of Table 2, an individual was considered cruciform if its lateral wings or humps were at least as angular as in Fig. 14-F, I. Unmodified ampulliforms never pos-

sessed embryos with more than the modest beginnings of lateral humps.

Larger ampulliforms, measuring up to 900–1,000 μ long and possessing trophi up to 140 μ , rarely 160 μ , long appeared in most if not all treated ponds. Such a large ampulliform developing in the uterus of a small ampulliform is shown in Fig. 14-E. Of the ampulliforms, only these larger ones were ever cannibalistic. At various times in L-2, L-4, and H-2 ampulliforms with trophi 80–130 μ long were found possessing embryos with trophi measuring 160–200 μ . The most extreme instance was a small ampulliform ($l = 600 \mu$, $t = 90 \mu$) that contained an embryo with trophi 200 μ long (July 1, L-2). It was not possible to determine directly whether these large-jawed embryos of small parents were ampulliform or campanuliform; but no known ampulliform was ever observed to possess trophi more than 160 μ in length. Furthermore, in L-4 on June 28 and July 1 and 2, there existed a more or less continuous spectrum of morphotypes, from 400 μ long ampulliforms to 1,000 μ long ampulliforms to 800–1,000 μ long campanuliforms bearing trophi 160–230 μ long. Although sometimes of the same size, the campanuliforms and large ampulliforms in this pond were distinguishable from each other by the relatively broader corona of the campanuliforms.

Cruciform individuals were distinctly more common in high dose than in low dose ponds (Table 2). With a single exception, no cannibalistic cruciforms were found. Cruciforms were produced not only by the various sizes of ampulliforms but also by campanuliforms and consequently were quite variable in both size and shape. The large (1,000–1,400 μ) campanuliforms in L-4 on July 8 possessed large trophi (200–250 μ long), but when they contained embryos these usually were similar to Fig. 14-H, L in shape and had rather small trophi (120–140 μ long). Individuals essentially identical to Fig. 14-H sometimes possessed embryos with the form of Fig. 14-J. Trophi of cruciforms generally were 90–130 μ long (Fig. 15-D), larger trophi usually being found only in cruciforms produced by campanuliforms. Cruciforms were responsible for most of the resting eggs produced (Table 2); usually not more than one and never more than two resting eggs were present in a cruciform individual. Most often cruciforms, like the other morphotypes, reproduced parthenogenetically, but nowhere near as rapidly as did small ampulliforms. Cruciforms frequently were devoid of embryos and rarely possessed more than two or three at one time. These offspring were usually cruciform also, but occasionally very large cruciforms produced campanuliform individuals (e.g., Fig. 14-F).

Campanuliforms, characterized primarily by a corona relatively much broader than that of ampulli-

forms, ranged from 700 μ to 1,500 μ in length and possessed trophi 160–280 μ long (Fig. 15-A, B, C). They were most frequent in L-4 and the high dose ponds and achieved their greatest abundances (relative to other morphotypes) in the latter part of the experiment at times when *Asplanchna* populations were declining or at least not increasing rapidly. As previously indicated, campanuliforms were produced, albeit rarely, by both ampulliforms and cruciforms. The parthenogenetic offspring of campanuliforms were usually other campanuliforms (Fig. 14-A) and, as we have said, occasionally cruciforms or campanuliform-cruciform intermediates. Campanuli-

forms were not as likely to produce resting eggs as were cruciforms (Table 2), but when they did, they did it on a larger scale, averaging two to four per individual. Five to six were found in several individuals (e. g., Fig. 14-B).

Campanuliforms were intensely cannibalistic on many occasions (Table 2). The trophi found in their stomachs ranged in length from 90 μ to 230 μ ; the weak correlation of trophi size with body size and shape precluded attempts to determine whether an individual's morphotype bore any relation to that individual's chances of being cannibalized. Although one was the rule, two to three trophi per stomach

TABLE 2. Polymorphism, cannibalism, sex ratio, and reproduction of *Asplanchna brightwelli* populations in insecticide-treated ponds

Pond and date	<i>Asplanchna</i> per 40 liters		Females			Percentage with resting eggs		Number <i>Asplanchna</i> examined
	Prev. date	Pres. date	Males (%)	Ampull. ^a (%)	Cruc. (%)	Campan. (%)	'Cruc.	
Pond L-1								
June 7	0 –	74	0	100	0	0	—	56
June 21	5 –	246	0	96	0	4	—	86
July 8	4 –	157	3	4	82	12 (16)	1	108
Pond L-2								
June 7	14 –	147	0	93 (1) ^b	7	0	0	129
June 14	13 –	91	0	2 (50)	84 (1)	14 (71)	12	119
June 19	10 –	113	0	100	0	0	—	62
June 24	6 –	170	0	100 (1)	0	0	—	179
July 1	8 –	150	0	100	0	0	—	80
July 2	150 –	763	1	98	0	2	—	150
July 19	0 –	183	0	100	0	0	—	78
							(ampull: 1%)	
							(ampull: 5%)	
Pond L-3								
June 10	2 –	43	0	100	0	0	—	53
June 14	43 –	56	0	17	71	12	0	77
July 19	1 –	58	0	32	25	43	0	28
Pond L-4								
June 10	57 –	250	0	7	40	53 (38)	30	103
June 24	2 –	110	0	71	7	22 (27)	0	69
June 28	110 –	69	0	97	0	3	—	62
July 1	69 –	280	0	95	0	5 (33)	—	68
July 2	280 –	357	2	98 (2)	0	2 (70)	—	333
July 5	357 –	254	1	0	3	97 (1)	0	118
July 8	254 –	193	0	0	10	90 (4)	0	93
July 19	32 –	1,287	1	100	0	0	—	181
July 26	1,287 –	180	0	100	0	0	—	116
							(ampull: 1%)	
Pond H-1								
June 21	25 –	71	0	36	46	18	0	11
July 19	0 –	387	2	0	75	25 (52)	13	124
July 26	387 –	1,267	2	0	96	4 (60)	6	136
August 7	1,267 –	380	1	0	13	87 (2)	18	130
Pond H-2								
June 7	0 –	77	0	100	0	0	—	92
June 14	11 –	126	0	28 (5)	69	3 (33)	0	72
June 24	3 –	213	0	90	8	2 (50)	0	119
July 1	1 –	178	4	45	53	3	0	216
July 2	178 –	703	10	13 (6)	81	6 (42)	16	589
July 5	703 –	463	2	0	67	33 (33)	28	302
July 12	36 –	320	0	0	7	93	0	124
July 19	320 –	953	3	0	27	73	20	160
July 26	953 –	210	0	0	21	79	0	159

TABLE 2—continued

Pond and date	<i>Asplanchna</i> per 40 liters		Females			Percentage with resting eggs		Number <i>Asplanchna</i> examined
	Prev. date	Pres. date	Males (%)	Ampull. ^a (%)	Cruc. (%)	Campan. (%)	Cruc.	
Pond H-3								
June 7	2 —	539	1	84 (15)	26	0	0	—
June 28	0 —	423	3	94	6	0	0	36
July 1	423 —	423	0	0	74	26 (36)	2	1
July 2	423 —	140	0	0	41	59 (18)	0	0
July 5	140 —	200	0	0	9	91 (8)	0	0
July 8	200 —	313	0	0	23	77 (2)	0	128
July 12	313 —	397	12	0	33	67	14	4
July 19	397 —	583	1	48	52	0	0	199
July 26	583 —	1,469	4	1	86	13 (11)	16	0
Pond H-4								
June 10	43 —	167	0	3	82	15 (4)	20	4
June 19	15 —	107	0	91	9	0	0	65
June 21	107 —	200	6	3	70 (3)	27 (43)	26	0
July 1	0 —	77	0	32	68	0	0	41
July 2	77 —	139	3	7	75	18 (14)	0	0
July 5	139 —	101	0	0	45	55 (14)	3	0
July 8	101 —	256	0	0	42	58 (2)	0	106
July 19	1 —	373	8	0	72	28	13	21
July 26	373 —	460	2	0	61	39 (11)	4	128
								194

^aMorphotype abbreviations: ampull. = ampulliform; cruc. = cruciform; campan. = campanuliform.

^bNumbers in parentheses represent the percentages of individuals that were cannibalistic, i.e., that had *Asplanchna* trophi in their stomachs.

were not uncommon (Fig. 14-A) and a few gluttons contained five.

Males lacked trophi and were always cruciform. Those that appeared during the first part of the experiment had a form not too different from that of the females in Fig. 14-J, K and a "wingspread" (maximum width) of 600–900 μ . In contrast, males appearing in high dose ponds during the second half of July showed extreme development of the cruciform morphology, resembling stout-bodied airplanes, and had wing spreads of 1,000–1,200 (Fig. 14-M). Male embryos were observed only in cruciform females, and more frequently in those with weakly developed (e.g., Fig. 14-I) than in those with well-developed wings (e.g., Fig. 14-K). However, their presence at times when cruciform females appeared to be absent (e.g., L-2 and L-4, July 2) suggested that they may sometimes have been produced by other morphotypes.

Examination of the stomach contents of roughly 1,500 *Asplanchna* representing 39 different samples (= pond-dates) indicated that small rotifers were the principal food supply for all *Asplanchna* morphotypes. Virtually every species of small rotifer found in the plankton was found at least once in an *Asplanchna* stomach. Isolated trophi in *Asplanchna* stomachs usually were not identified, but the rigid loricas, e.g. of *Brachionus*, *Monostyla*, *Tripleuchlanis*, etc., were identified to species. *Hexarthra*, *Polyarthra*, and *Filinia* could sometimes be detected in *Asplanchna* stomachs by their setae or appendages.

The mean number of small rotifer trophi per *Asplanchna* gut was generally correlated with the size of the small rotifer population. When small rotifers were scarce, the stomachs of many *Asplanchna* were empty or contained other types of prey. When small rotifers were abundant, it was not uncommon to find *Asplanchna* containing remains of 5–10 small rotifers, and one individual contained remains of 26–1 *Tripleuchlanis*, 10 *Hexarthra*, and 15 unidentified trophi. *Asplanchna* showed a decided preference for the spineless *B. angularis* over the four-spined and slightly larger *B. budapestinensis* whenever all three species were abundant enough to test for this possibility (Table 3, Fig. 12-A, B). Nevertheless, when the even larger and more heavily spined *B. bidentata* (Fig. 12-H) was the only abundant rotifer (Fig. 13; L-4, June 24 and July 19), the majority of *Asplanchna* were found to contain one to three *B. bidentata* each. Presumably ingested when still attached to the parent, the eggs of small rotifers averaged more than one per *Asplanchna* stomach in six of the 39 samples examined. In view of their high nutrient content, these eggs are a valuable supplement to *Asplanchna*'s diet when the small rotifers are actively reproducing. Even *Asplanchna* resting eggs were found in a few *Asplanchna* stomachs—a result of cannibalism.

Sometimes when small rotifers were scarce, crustaceans became an important, even dominant, item in *Asplanchna*'s diet. Copepod nauplii were eaten occasionally by all *Asplanchna* morphotypes, but cope-

TABLE 3. Relative abundances of *Brachionus angularis* and *B. budapestinensis* in *Asplanchna brightwelli* stomachs and in the plankton. On each date *B. budapestinensis*, relative to *B. angularis*, was significantly ($P < 0.001$) underrepresented in *Asplanchna* stomachs, as indicated by chi-squared tests of the data in columns 1 and 2

Date and pond	Number/liter	Total number found in <i>Asplanchna</i>	Number <i>Asplanchna</i> with 1+	
			Number <i>Asplanchna</i> examined	Number <i>Asplanchna</i> with 1+
June 7, H-2				
<i>B. angularis</i>	1,171	24	12/18	
<i>B. budapestinensis</i>	1,108	4	3/18	
June 24, L-2				
<i>B. angularis</i>	32	89	33/40	
<i>B. budapestinensis</i>	26	4	2/40	
June 24, H-2				
<i>B. angularis</i>	303	35	14/23	
<i>B. budapestinensis</i>	199	0	0/23	
July 1, L-2				
<i>B. angularis</i>	105	38	23/47	
<i>B. budapestinensis</i>	409	4	4/47	

podites (length = 800–1,200 μ) were, with few exceptions, found only in the stomachs of campanuliforms. The ingestion of *Diaptomus* depicted in Fig. 12-C probably occurred during the interval between the collecting of the plankton sample and the addition to it of formaldehyde; copepods found in *Asplanchna* usually were completely within the stomach and sometimes partially disarticulated. On June 10 in L-4 *Cyclops* was abundant (Fig. 5), small rotifers were scarce (Fig. 10), and 60% of *Asplanchna* campanuliforms contained *Cyclops* copepodids although less than 10% of all morphotypes contained remains (trophi, loras) of small rotifers. Three of the campanuliforms contained two copepodids apiece. Copepodids of *Cyclops* or *Diaptomus*, or both, were eaten in lesser numbers by *Asplanchna* campanuliforms in L-2 (June 7), L-3 (June 14), L-4 (July 1, June 24), H-2 (June 14, July 2), H-3, (July 26), and H-4 (June 10, July 26). Cladocerans were rarely found in *Asplanchna* stomachs, but probably only because cladocerans and *Asplanchna* were rarely present at the same time. However, *Moina* was found in 40% and 10% of the campanuliform *Asplanchna* present in H-1 on August 7 and in H-2 on July 26, respectively.

Insects, previously unknown in the diet of *Asplanchna*, were found in the stomachs of seven campanuliforms. One contained a chironomid larval head capsule (width = 200 μ), one an entire chironomid larva (length = 750 μ), and five (from H-1 on July 19 and 26, and H-2 on July 5) contained tiny mayfly (Ephemeroptera) nymphs ranging in length from 400 μ to 900 μ , exclusive of caudal filaments.

In certain instances *Asplanchna* stomachs contained algae which, by their size, intact condition, and lack of association with remains of small rotifers, were judged to have been ingested by *Asplanchna* directly and not via the stomachs of small rotifers. Pennate diatoms 75 μ in length were found in nine out of 26 *Asplanchna* examined from L-4 on June 24; these nine averaged 13 diatoms each. One individual from H-2 on June 14 contained eight diatoms 30 μ long, which probably had been ingested as a single unit. *Asplanchna* from L-2 on July 2 gave no evidence of feeding on the 25 μ long *Synedra* sp. even though this phytoplankton was exceedingly abundant on that date (Fig. 8). Two *Asplanchna* from H-4 on July 8 contained, respectively, approximately 20 and 70 *Pandorina* colonies (diameter = 20 μ). The flagellate *Trachelomonas*, 20–30 μ long, was occasionally found in *Asplanchna* from H-1 and on July 19 averaged 1.5 per *Asplanchna* with some individuals containing as many as five. Heterocysts, spores, and short filaments of *Anabaena* spp. were found in small to moderate amounts in six of 19 *Asplanchna* from H-3 on July 1 and in eight of 26 *Asplanchna* from H-2 on July 2. In the first instance, the *Asplanchna* contained many trophi and could have ingested *Anabaena* indirectly via the gut of, for example, *Hexarthra*. In the second instance, *Anabaena* was more abundant in *Asplanchna* individuals without small rotifer trophi than in those with such trophi. For some *Asplanchna* in high dose ponds in late July *Pediastrum* coenobia were a conspicuous food item (e.g., Fig. 12-A). They were found in the stomachs of 43% of the *Asplanchna* in H-1 on July 19, of 11% in H-2 on July 19, of 25% in H-3 on July 26, and less often on other occasions. Pollen grains and the tests of testaceous rhizopods were found in perhaps two dozen of the 1,500 *Asplanchna* examined.

DISCUSSION

This study, in addition to ascertaining the effects of a particular insecticide on pond ecosystems, presented the opportunity to observe the interrelations of the species present as revealed in their response to disturbance of the system and their recovery from it. The results will be discussed primarily from the latter point of view, and their implications for the use of Dursban (and insecticides generally) will be noted. We will make the assumption that the insecticide Dursban had no direct effect other than mortality on any organisms or, if it did, that it was overshadowed by indirect effects. In particular, it is assumed that the posttreatment population increases observed for certain species resulted not from a direct stimulation of reproductive physiology by the insecticide but rather from the mortality of predators or competitors. This attitude is evident in Table 4, where

TABLE 4. Summary of short-term population responses to Dursban treatment and postulated causes

Population	Cause
Populations which decreased following treatment	
<i>Cyclops</i>	Toxicity of Dursban
<i>Moina</i>	Toxicity of Dursban
Herbivorous insects	Toxicity of Dursban
Predaceous insects	Toxicity of Dursban (and reduction of prey? - herbivorous insects, crustaceans)
Benthic rotifers	Toxicity of Dursban (high concentrations in sediments)
<i>Schroederia</i>	Increase in competitors (other phytoplanktoners)
Populations which increased following treatment	
<i>Diaptomus</i>	Reduction of predators (<i>Cyclops</i>)
Planktonic rotifers	Reduction of competitors (<i>Moina</i>) and of predators (<i>Cyclops</i>)
<i>Asplanchna</i>	Increase in prey (small rotifers) and reduction of predators (predaceous insects)
Phytoplankton	Reduction of grazers (crustaceans)

we list the principal increases and decreases and what we conceive to be their most probable causes. The trophic relationships of the populations are summarized in a simple food web as an aid to discussion (Fig. 16).

Role of predaceous insects

Predaceous insects were the top predators or highest trophic level in the ponds and presumably had a dominant influence, direct or indirect, on all other populations. Our data do not permit a detailed analysis of this influence, but certain correlations and possibilities may be noted.

Reduction of cladoceran populations by predaceous insects may have permitted the development of large populations of small rotifers in control ponds in early July and mid-August (Fig. 3, 5, 10). Elsewhere we have seen *Buenoa* sp. and *Laccophilus* spp. seizing and eating cladocerans. Selective attack by such predators on the larger, perhaps more easily seized *Moina* could also have been a factor encouraging development of *Ceriodaphnia* populations; mature *Moina* females measured 850 to 1,300 μ in total length and those of *Ceriodaphnia* only 400 to 500 μ .

The failure of *Asplanchna* to respond to prey (i.e., small rotifer) populations in control ponds may have reflected the susceptibility of this organism to insect predation. We have no direct evidence of such predation, but *Asplanchna* appears to be of a suitable size (mostly 700–1,200 μ long) and is without any particular defenses against predaceous insects. If this explanation is valid, then the large populations of *Asplanchna* in treated ponds were as much the result of decreased numbers of predaceous insects as they were of increased numbers of small rotifers.

An important principle suggested by the interaction of predaceous insects with other populations is that the long-term effects of an insecticide in an ecosystem will be largely determined by its effects on the top predators of that ecosystem, in particular, whether none, some, or all of these top predators are killed. For example, in ponds where the mosquito-fish *Gambusia affinis* is top predator, it feeds on and keeps zooplankton populations at low levels, thereby permitting development of large phytoplankton populations (Hurlbert, Zedler, and Fairbanks 1972). If these *Gambusia* populations were to be completely eliminated by an insecticide treatment, ultimate effects would include increased zooplankton and decreased phytoplankton populations, i.e., effects just the reverse of those in an ecosystem with one less trophic level. If still higher trophic levels, e.g., piscivorous fish, birds, and mammals, are present, insecticide treatment could have any one of many effects, depending on which predators suffered mortality and to what extent.

Cyclops as predator

Copepodids of *Cyclops* (*Acanthocyclops*) *vernalis* can be "markedly carnivorous" as evidenced by the remains of copepods, cladocerans, and rotifers in their digestive tracts (Fryer 1957). This probably accounts for the striking inability of *Diaptomus* populations to increase in the presence of *Cyclops* populations of more than a small size, and perhaps also for the slightly weaker negative correlation between *Cyclops* and *Moina* (Fig. 5). At least two cyclopoid copepods, *Cyclops strenuus abyssorum* (Fryer 1957) and *Cyclops biscuspisidatus thomasi* (McQueen 1969), are known to prey preferentially on diaptomids, especially their nauplii, relative to cladocerans. *Moina*, and cladocerans in general, which have a carapace and retain the developing young in a brood chamber, may be less subject to cyclopoid predation.

The *Cyclops*-rotifer interaction probably was complex. Elsewhere we have observed *Cyclops vernalis* seize the rotifer *Keratella quadrata* by its anterior spines, reach into its lorica and make circular motions with an anterior pair of appendages, and sweep the rotifer's tissues into its mouth, discarding the lorica. Presumably, *Cyclops* preyed on at least some rotifers in the present study. On the other hand, *Cyclops* nauplii feed on the smaller phytoplankton (Ruttner 1963) and possibly compete with herbivorous rotifers. Thus the increase in herbivorous rotifers after the second treatment of L-1 and L-4 and the negative correlation on May 28 between *Cyclops* nauplii and copepodids on the one hand and herbivorous rotifers on the other (Fig. 5, 6, and 10) could have reflected decreased competition, decreased predation, or both. *Cyclops* may not have been effective

in either role, however, since a considerable degree of coexistence of *Cyclops* nauplii and copepodids and rotifers was observed in C-1, C-4, and L-4 at certain times in July and the rotifer population in L-1 was already increasing rapidly, despite the presence of *Cyclops*, when the second treatment was made.

Crustacean-rotifer competition

The competition between rotifers and cladocerans for the bacterioplankton and smaller phytoplankton (Brooks and Dodson 1965) probably explains the negative correlation between the two groups. Cladocerans generally dominated in the control ponds because, in the absence of predators that feed preferentially on larger zooplankters, size and competitive ability are positively correlated. Rotifers dominated in treated ponds because they were less susceptible to the insecticide and were capable of rapid population increases once their competitors (and predators) had been eliminated. The exact mechanism whereby cladocerans depress rotifer populations is still unknown.

The negative correlation between *Diaptomus* and *Polyarthra* populations is also interpreted as a result of competition. Unlike the other planktonic rotifers encountered in this study, *Polyarthra* feeds only on cells more than 15 μ long (Dieffenbach and Sachse 1911, Edmondson 1965, Pourriot 1965b). Thus it would be more likely to compete with *Diaptomus* copepodids, which are coarse-particle filter feeders (Malovitskaya and Sorokin 1961). It is notable that the rotifer that coexisted most successfully with *Diaptomus* was *Filinia* (in L-3, Fig. 5, 13), which is known to feed on only the smallest of phytoplankters (Pourriot 1965b, Hutchinson 1967).

The dependence of *Polyarthra* on phytoplankton larger than 15 μ may also have been responsible for its lesser abundance in treated than in control ponds. Following reduction of crustacean grazing pressure by insecticide treatments, these larger cells must have multiplied more slowly than the smaller cells on which other rotifers depended, if we assume a general inverse relationship between cell size and generation time. This set a limit to the rate at which *Polyarthra* populations could increase. By the time these larger cells had become abundant, *Asplanchna* was also abundant, having increased in response to the fast-developing populations of other rotifers. Apparently for *Polyarthra* the advantages of an increased food supply were soon more than canceled out by increased *Asplanchna* predation and increased competition with *Diaptomus*.

Benthic versus planktonic populations

The differential effect of treatment on benthic versus planktonic rotifers may have resulted from (1) a

greater physiological susceptibility of benthic rotifers to Dursban, (2) greater concentrations or persistence of Dursban in the benthic than in the planktonic habitat, (3) deleterious effects of the phytoplankton blooms on the food supply of benthic rotifers, or any combination of these factors. There is little basis on which to choose among these alternatives. However, the concentration of Dursban in water, where it is mostly sorbed on particulate matter, decreases rapidly with time, whereas its concentration in bottom sediments increases to a maximum 1–2 weeks following treatment; at 4 hours, 1 day, and 14 days, respectively, after treatment, the concentration of Dursban in the upper 5 cm of sediment probably was approximately $\frac{1}{2}$, 10, and 50+ times greater than its concentration in the water on those same days (Table 6 in Hurlbert et al. 1970). Clearly benthic rotifers were exposed to Dursban of generally higher concentrations and for longer periods of time than were planktonic rotifers.

The same consideration may account, in part, for the differing abilities of *Cyclops* and *Diaptomus* to survive Dursban treatments. Cyclopoid copepods are mostly benthic-littoral in habit, whereas calanoid copepods are generally more planktonic (Wilson and Yeatman 1959, Hutchinson 1967).

Asplanchna population dynamics

The most interesting consequences of insecticide treatment were found in *Asplanchna brightwelli*. As a context in which to discuss these effects, salient features of the life history of *Asplanchna* are summarized in Fig. 17. All features of this scheme were observed by Powers (1912), and most have been confirmed by later investigators and by our own data. Each morphotype (although not each individual) is capable of parthenogenetically producing young of its own morphotype and of at least one of the other two morphotypes. In the transition to a new morphotype sometimes, but not always, one or more generations of intermediate morphotypes intervene. All morphotypes can produce resting eggs and males, but,

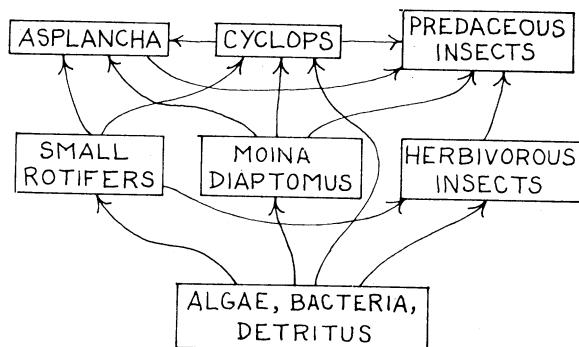


FIG. 16. A condensed and simplified diagram of the food web of experimental ponds. Arrows lead from food to feeder.

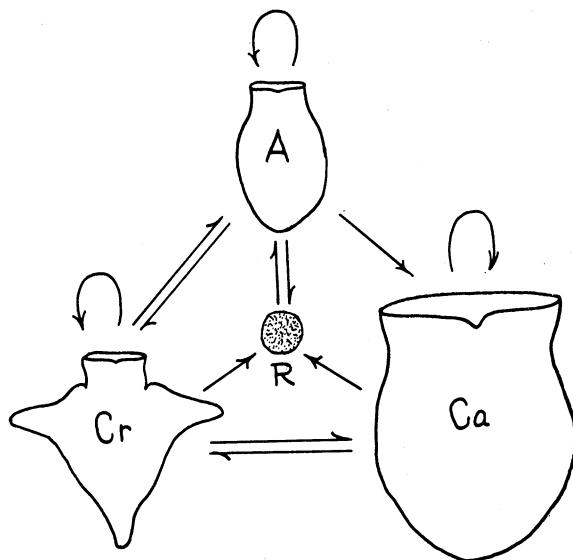


FIG. 17. Reproductive and transformation options in the life cycle of *Asplanchna brightwelli*. A = ampulliform, Cr = cruciform, Ca = campanuliform, R = resting egg. Except for those associated with the resting egg, all arrows represent parthenogenetic reproduction. Looped arrows indicate parthenogenetic production of young having same morphotype as parent. The various intermediate morphotypes possible are not shown.

on hatching, all resting eggs yield ampulliform individuals (Powers 1912).

Size, sexual reproduction, and polymorphism of *Asplanchna* populations were especially affected by treatment. Although the large increases in *Asplanchna* populations of treated ponds were fostered by increases in populations of herbivorous rotifers, the exact numerical relations of *Asplanchna* and its prey were variable, probably reflecting insect predation, the varying species composition of the prey-rotifer population, and *Asplanchna*'s flexible life history. Variability in sizes, morphotypes, and reproductive abilities of individuals would be expected to cause equal variability in responses of *Asplanchna* to prey populations. Ampulliform individuals, for example, reproduced at a more rapid rate, but probably consumed fewer prey per unit time than did campanuliform individuals. Switching from parthenogenetic to sexual reproduction undoubtedly modulated *Asplanchna* population fluctuations by slowing the rate of parthenogenetic reproduction and by producing resting eggs, which hatch only after a dormant period. According to circumstances, such modulation may have either increased or decreased the closeness with which *Asplanchna* populations "tracked" their prey populations.

The highest rates of sexual reproduction, as evidenced by the presence of males and resting eggs, generally occurred in the high dose ponds, and only in those ponds (H-2, H-3, H-4) that experienced

blooms of *Anabaena* did males ever compose more than 3% of the population (Table 2, Fig. 8). In these ponds *Asplanchna* stomachs sometimes contained *Hexarthra* and *Hexarthra* guts often contained *Anabaena*. Possibly *Anabaena*, like many other kinds of algae, synthesizes vitamin E, a substance required by *Asplanchna* for sexual reproduction (Birky 1968, Gilbert 1968). The adaptive significance of this dependence on vitamin E may relate to Edmondson's (1957) observation, made in reference to production of males by *Moina* populations, that since "algae accumulate lipid [vitamin E is a lipid] in a nitrogen-deficient medium (Fogg and Collyer 1953), . . . the appearance of excess lipid could signal the approach of unsatisfactory conditions." In whatever respect the conditions might be unfavorable, the production of resistant eggs requiring diapause usually permits the population to survive until conditions improve. Any general explanation of *Asplanchna*'s sexuality must also consider Birky's (1969) demonstration that high population density increases the sensitivity of *Asplanchna* to vitamin E and his suggestion that population density is the effective determinant of time of sexual reproduction, since sufficient levels of vitamin E probably are available in *Asplanchna*'s diet through the year.

Asplanchna cannibalism and polymorphism

No investigator has speculated on the adaptive significance of polymorphism in *Asplanchna*; efforts have been directed only toward elucidating the proximate physiological factors responsible for the transformations. We propose that each of the three basic morphotypes is especially adapted to survive in or exploit, or both, one particular type or class of environmental condition(s); and that, as indicated primarily by the work of Birky (1968, 1969) and Gilbert (1968, 1969), the species has evolved a fine mechanism, involving sensitivity of embryological development to specific chemicals encountered in its diet and environment (including chemicals released into the environment by *Asplanchna* itself) for producing the morphotype(s) most appropriate for any given set of conditions. Significant features of the morphotypes may be summarized as follows:

- 1) Ampulliform individuals are small, morphologically simple, produce young at a rapid rate, presumably have a short generation time, and thus are well adapted to conditions of high food abundance under which they can produce a larger population sooner than could either of the other morphotypes.

- 2) Campanuliform individuals are large, capable of capturing larger prey (e.g., cladocerans, adult copepods, insect larvae and nymphs) than are the other morphotypes, and would be at an advantage when such large prey are the principal or only prey available.

3) Cruciform individuals are equipped with four humps or body-wall outgrowths (posterior, postero-dorsal, and two lateral), which probably serve to thwart cannibalistic attacks by other individuals in the population, and give cruciform individuals an advantage over ampulliform individuals when cannibals, such as campanuliforms, are present.

Some of the above are interpretations rather than observations. We now consider the facts and arguments supporting these, and describe what is known of the mechanisms that integrate them into a highly flexible strategy for exploiting environmental resources.

To take advantage of rapidly increasing and often ephemeral prey populations, *Asplanchna* must be capable of rapid increases also. Accordingly, the early development of all *Asplanchna* populations appeared to be dominated by ampulliforms (Table 2), which had a reproductive rate, as measured by the proportion of individuals containing embryos and by the mean number of embryos per individual, unquestionably greater than that of either of the other morphotypes. The principal mechanism ensuring dominance of ampulliforms in the early stages of population growth is the consistency with which resting eggs yield only ampulliform individuals (Lange 1911, Powers 1912). The ampulliform morphotype can be maintained for an indefinite number of generations and undergoes transformation to other morphotypes only when stimulated by changes in specific environmental factors (Powers 1912, Birk 1968, 1969, Gilbert 1968, 1969, Gilbert and Thompson 1968).

The demonstrated ability of campanuliform individuals to capture larger prey, such as crustaceans, may or may not entail some sacrifice in ability to utilize smaller prey such as protozoans. One suspects that large trophi (e.g., Fig. 15A, B) would have difficulty seizing individual prey having linear dimensions on the order of, say 50 μ ; and that populations polymorphic with respect to body and trophi size are able to utilize a greater variety of organisms as prey than are populations monomorphic in these respects. The ability of campanuliforms to feed on crustaceans is especially significant in view of the negative relationship between the abundance of herbivorous rotifers and cladocerans (Fig. 11), which probably is a widespread phenomenon. If the development of a crustacean population occasions the demise of herbivorous rotifer populations, *Asplanchna* can switch to a larger morphotype and continue to thrive. Powers (1912) observed just such a case in a pond where cruciform and large ampulliform individuals began feeding on *Moina* following the decline of *Brachionus* and *Hydatina*, and, within 9 days, gave rise to a population composed almost entirely of campanuliform individuals. Powers (1912) maintained campanuliform-dominated cultures in the laboratory for many

weeks on a diet consisting solely of *Moina*. In our own ponds the situation was not always so simple; for example, campanuliform individuals became abundant in H-3 and H-4 well before the crustacean populations recovered from treatment (Fig. 5, Table 2).

The proximate causes of the appearance of campanuliform individuals in a population are unknown. Powers (1912) claimed that cannibalism and feeding on *Moina* led to the production of campanuliforms. His observations did not completely preclude other interpretations, however, e.g., that cannibalism and *Moina*-feeding were results, not causes of the appearance of campanuliforms.

Powers (1912) felt that in natural populations campanuliforms rarely amounted to more than 1% of the total population. Absence of the appropriate stimuli is the simplest interpretation. Also, campanuliforms perhaps are more susceptible to predation by insects and zooplanktivorous fish than are the two smaller morphotypes, and may sometimes be rare for that reason alone.

The proposition that the wings or humps of cruciform individuals have evolved and function specifically as anticannibalism devices is supported by much circumstantial evidence. First, there is the remarkable similarity between the wings of *Asplanchna* and the postero-lateral spines of *Brachionus calyciflorus*. These spines are produced when *B. calyciflorus* is exposed to certain unidentified substances released into the environment by *Asplanchna*. The spines afford *B. calyciflorus* a significant measure of protection from *Asplanchna* predation (Beauchamp 1952a, b, Gilbert 1967). When these animals swim undisturbed, the posterolateral spines of *B. calyciflorus* extend straight backwards and the wings of cruciform *Asplanchna* are retracted, but when disturbed or on colliding with certain types of foreign objects, the corona is withdrawn creating pressure within the body cavity and causing lateral extension of the wings of *Asplanchna* or the spines of *Brachionus* and a large increase in effective diameter of the organism (Plate 1886, Powers 1912, Wesenberg-Lund 1930, Gilbert 1967, Gilbert and Thompson 1968). This similarity in operation suggests similarity of function.

Second, while *Asplanchna* predation is minimized by the spines of *B. calyciflorus*, it seems unlikely that insect or fish predation is going to be hindered by the wings of *Asplanchna*, and other organisms are not likely predators on *Asplanchna*. On the other hand, cannibalism does occur in *Asplanchna*, sometimes with high intensity, and there is no reason why *Asplanchna* should not have evolved mechanisms for minimizing it very similar to the anti-*Asplanchna* mechanisms evolved by *B. calyciflorus*. Beauchamp (1951), noting similarities between the seemingly

chaotic variability of spine length in brachionid rotifers and of morphotype in *Asplanchna*, once concluded: "L'explication de l'un, quand elle sera trouvé, sera sans doute valable aussi pour l'autre . . ." Nevertheless, since he never found cannibalism to be frequent in populations he examined, he was not led to consider it as a possible factor, even when he later discovered (Beauchamp 1952a, b) *Asplanchna*'s effects on spine length in *B. calyciflorus*.

Third, the cruciform morphotype occurs in its most extreme form and with the highest frequency exactly in those instances where the potential for cannibalism is greatest: (1) In those samples where campanuliforms, the most cannibalistic morphotype, composed less than 10% of the total, cruciforms outnumbered ampulliforms only 24% (= 6/25) of the time; but in those samples where campanuliforms composed more than 10% of the total, cruciforms outnumbered ampulliforms 93% (= 26/28) of the time (Table 2). This difference is highly significant ($P < 0.001$). (2) Parthenogenetically, campanuliforms produce campanuliforms and cruciforms, but never ampulliforms, which presumably would be cannibalized almost as soon as they appeared. The cruciforms so produced by campanuliforms show extreme development of the lateral wings which have a spread often in excess of the animal's length (Powers 1912). (3) Males, because they typically are produced only at high population densities and must seek out and copulate with females (= potential cannibals) and because of their generally smaller size, are particularly subject to cannibalism. Accordingly, all males are cruciform and generally to a more extreme degree than the females with which they coexist (Fig. 14-M).

We find this evidence that cruciformity is an adaptation for avoiding cannibalism to be compelling. That appreciable cannibalism by campanuliforms sometimes occurred even when cruciforms were the dominant morphotype (Table 2) is no contradiction to our argument; presumably even more cannibalism would have occurred if ampulliforms had been dominant.

Following the conservative taxonomy adopted by Gilbert (1968), we have taken *Asplanchna brightwelli* Gosse to include forms designated as *A. sieboldi* Leydig and *A. intermedia* Hudson. The more recent tendency, however, has been to treat *A. sieboldi* as a separate and valid species (Gilbert and Thompson 1968, Birk 1969). If that more accurately reflects the biology of the situation, and it probably does, then the distinct tooth on the scapus (Fig. 15) and the rampant polymorphism (Fig. 14) of our populations assign them to *A. sieboldi*.

Algal blooms

Recent studies have shown that DDT and other

organochlorine insecticides in concentrations as low as 10–20 ppb are capable of causing a 50% reduction in the photosynthesis or population growth of various planktonic algae (Ukeles 1962, Wurster 1968, Menzel, Anderson, and Randtke 1970). These led to predictions that in insecticide-contaminated aquatic ecosystems the total phytoplankton population may decline (Wurster 1968) or that the relative abundances of algal species will be altered as a result of interspecific variation in susceptibility (Wurster 1968, Menzel et al. 1970). Such extrapolations neglect accumulating evidence that crustacean zooplankters are, in general, more susceptible to DDT than are phytoplankters (Anderson 1960, Sanders and Cope 1966, Grosch 1967) and that grazing by such zooplankters is often a significant factor limiting the size and species composition of phytoplankton populations (Pennington 1941, Edmondson 1957, Hrbacák et al. 1961, Hrbacák 1964, Lund 1965).

We expect that a common result of insecticide treatment of aquatic ecosystems will be increase of phytoplankton populations following mortality of zooplankton populations and, further, that those changes that do occur in the relative abundances of phytoplankton species are more likely due to alterations in grazing pressure than to interspecific variations in insecticide susceptibility. The long-term effects on phytoplankton will be determined largely by how the higher trophic levels are affected by the insecticide. But to the extent that zooplankters are eliminated, phytoplankters armed with spines, digestion-resistant cell walls, or other defenses against zooplankters will no longer have any competitive advantage over simpler more edible phytoplankters, which probably are capable of more rapid population increase. Thus the *Schroederia* blooms in low dose ponds were delayed until *Moina* populations recovered from treatment (Fig. 5, 9) and, presumably, grazed down the smaller phytoplankters. Development and persistence of *Schroederia* populations also appeared to be inhibited by *Cyclops* copepodids, which, being raptorial, could have fed on this alga.

Previous reports of insecticide-induced algal blooms are few. The most significant, overlooked in recent discussions of insecticide effects, is Shane's (1948) report of repeated aerial applications of DDT (rate unspecified) made during September 1947 to the entire city of Wilmington, Delaware, including a 40-million-gallon water reservoir, to reduce the fly population and control a polio epidemic. Soon after treatment began, *Cyclops* and *Daphnia* disappeared from the reservoir and the diatom *Synedra* began increasing, eventually attaining a density of 10,000 cells/ml and averaging 5,000 cells/ml over the entire month of September, as compared with averages of 42–81 cells/ml for Septembers of the four preceding years. A subsequent lowering of water level

showed the walls of the reservoir to be encrusted with crystalline DDT. Similarly, Cook and Connors (1963) observed heavy *Anabaena* blooms and reduced crustacean zooplankton populations following three successive applications of methyl parathion at 3 ppb to Clear Lake, California; Kiser, Donaldson, and Olson (1963) reported heavy mortality of crustacean zooplankters and slight increases in phytoplankton following treatment of a lake with rotenone; and certain insecticides have been used prophylactically to maintain bloom conditions in open-air algal cultures that are subject to occasional invasion and depletion by copepods (Loosanoff, Hanks, and Gannaros 1957).

It is evident that insecticides are capable of aggravating eutrophication problems. Excessive algal production requires both a surfeit of nutrients and a paucity (or inefficiency) of herbivores. To the extent that they bear both nutrients and insecticides, waters draining from agricultural land pose a double threat in this respect.

The stimulation of *Anabaena* blooms by Dursban should be a matter of concern to those involved in mosquito control and other programs requiring insecticide treatment of aquatic habitats. *Anabaena* blooms and their associated bacterial populations can render the water of marshes, ponds, and lakes extremely toxic, and there are numerous recorded instances of livestock and wildlife dying after drinking from waters affected by such blooms (Schwimmer and Schwimmer 1968). Highly toxic environments can thus result from use of insecticides that are quite innocuous from a narrow toxicological point of view. Admittedly, in our study *Anabaena* blooms were induced only at treatment rates greater than those normally used; and the role of parathion in the Clear Lake *Anabaena* bloom was not unequivocally established. However, the potential has been demonstrated, and since few attempts have been made to observe insecticide-phytoplankton interactions, the lack of harder evidence is no testimony to innocence.

CONCLUSION

By stimulating algal blooms and reducing predaceous insect populations, Dursban created an ecological imbalance apparently favorable to the very insects it was meant to control. Algal blooms following use of DDT (Shane 1946) and parathion (Cook and Connors 1962) indicate that such effects are not unique to Dursban and frequently must follow application of any broad-spectrum insecticide to a fresh-water environment. The extent to which these effects aggravate mosquito-control problems obviously will vary according to circumstances. If toxic blooms of blue-green algae prove to be a frequent result of insecticide treatment, then the use made of a body of water by livestock and vertebrate wildlife

will be a second important factor determining whether a given insecticide treatment will cause more problems than it solves.

More favorably, the Dursban treatments provided numerous insights into phytoplankton-zooplankton, rotifer-crustacean, and prey-predator relationships and into the significance of polymorphism in *Asplanchna*. Clearly, insecticides and other poisons can be valuable tools for the experimental manipulation and investigation of aquatic ecosystems, as a few (e.g., Hrbáček and Novotna-Dvorakova 1965) have already recognized. It is the experimental approach, utilizing controls and replication, that is of greatest importance, however, since the manipulation of almost any variable, whether pesticide, fertilizer, water temperature, predator population, etc., is likely to yield highly interesting results and similar insights into the functioning of the control ("natural") ecosystems.

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