

Consequences of tadpole shrimp predation on mayflies in some Californian ponds

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SUMMARY. 1. During two, 1-month studies, the abundance of mayfly nymphs, *Callibaetis californicus* Banks, in small ponds that contained the tadpole shrimp, *Triops longicaudatus* (LeConte), often was significantly lower than in ponds without tadpole shrimps. Mayfly abundance was either positively correlated or not significantly associated with that of predacious insects.

2. Larger mayfly nymphs were a greater fraction of the population in ponds with *Triops* than in ponds without tadpole shrimps. Between 2 and 3 weeks after ponds were flooded, the smallest mayfly nymphs were absent from ponds in which *T. longicaudatus* densities were >5 individuals per square metre during the summer and >15 individuals per square metre during the autumn.

3. In prey-choice trials, *T. longicaudatus* consumed predominantly small *C. californicus* nymphs (mean headwidth ± 1 SD: 0.44 ± 0.05 mm). After encounters with tadpole shrimps, small mayfly nymphs moved relatively short distances, were easily overtaken, and were, consequently, more susceptible to tadpole shrimps than larger-sized nymphs.

Introduction

Predator–prey relationships in the aquatic systems of arid and semi-arid habitats are relatively unexplored as compared to those in mesic lakes and streams (Resh & Rosenberg, 1984; Dodson, 1987; Kerfoot & Sih, 1987). The tadpole shrimp, *Triops longicaudatus* (LeConte), occurs frequently in transient habitats throughout a broad geographical range that extends from the Americas and West Indies through the Indo-Pacific region (Linder, 1952; Longhurst,

1955a, b). In the Coachella Valley and the Central Valley of California, *T. longicaudatus* is commonly found in many man-made, transient habitats such as flood-irrigated agricultural fields (i.e. date gardens, rice fields) and the large, temporary ponds of wildfowl hunting clubs.

Tadpole shrimps are able to exploit unpredictable, ephemeral habitats because they produce eggs which resist drying and develop rapidly to the reproductive stage. Dormant eggs in the substrate may hatch up to 2 weeks after inundation; however, most eggs hatch within 1–3 days (Takahashi & Gohda, 1981; Anonymous, 1983). At 21°C, tadpole shrimps begin reproduction approximately 9–12 days

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after hatching (Scott & Grigarick, 1979a) and individuals lay predominantly dormant eggs which require desiccation prior to hatching (Takahashi, 1977; Scott & Grigarick, 1979b).

During development, *Triops cancriformis* (Bosc.) switch from a diet that consists primarily of microalgae and particulate organic matter to one that incorporates a variety of plant and animal material (Pont & Vaquer, 1986). Carnivory in *T. cancriformis* increased markedly between 1 and 2 weeks after hatching in rice fields in southern France (Pont & Vaquer, 1986). Animal remains were observed in 27% of digestive tracts of 5–10 mm (total length) *T. cancriformis* and in 93% of larger individuals (>10 mm total length). Tietze & Mulla (1989) found, however, that *T. longicaudatus* was carnivorous at smaller sizes. In laboratory experiments, tadpole shrimps as small as 2.2 mm (carapace length; total length is approximately 3 mm) consumed first and second instar mosquito larvae (Tietze & Mulla, 1989).

Because tadpole shrimps often attain densities of several hundred individuals per square metre, lay desiccation-resistant eggs, become carnivorous soon after habitats are inundated, and feed on mosquito larvae (Maffi, 1962; Tietze & Mulla, 1989), they have been proposed as a biological control agent for mosquitoes. *Triops* has the potential to reduce the populations of certain dipterans, such as culicine mosquitoes (Tietze & Mulla, 1989) and ceratopogonids (Dodson, 1987), and might also affect the abundances of other co-habiting insects. Here, we examine the association between *T. longicaudatus* and the commonly co-occurring mayfly, *Callibaetis californicus* Banks, in small ponds in the Coachella Valley of southern California. We also determine the size-structure of mayfly nymph populations in ponds with different *Triops* densities and, via prey-choice experiments in the laboratory, the size-related consequences of tadpole shrimp predation on *C. californicus*.

Methods

Study site

Tadpole shrimps and mayflies were studied in small ponds at the University of California-Riverside, Aquatic and Vector Control Research Facility located approximately 5 km

northwest of the Salton Sea in Oasis, CA (33°32'30"N, 116°06'56"W; 55 m BSL). The ponds are arrayed in an 8 × 8 grid and subsets of the ponds are used primarily for short-term (i.e. 1 month) studies of mosquito control and biology.

The ponds contained a mixture of bermuda [*Cynodon dactylon* (L.)], crab [*Digitaria sanguinalis* (L.)], and nut (*Cyperus* sp.) grasses. To standardize the height of vegetation at the start of each experiment, the vegetation was cut to approximately 6 cm and the cuttings were removed prior to inundation.

The water supply was extracted from a single well. Ground water was pumped into a holding tank and flowed to the ponds via an underground pipeline. Four pipelines branched perpendicularly from the main pipeline, each pipeline fed the ponds in a pair of rows (i.e. rows A–B, C–D, E–F and G–H) and the distance between ponds in each of the four pairs of rows was <3 m. The distance between adjacent pairs of rows (i.e. B vs. C, D vs. E, etc.) was 8.5–11 m. For the columns (i.e. 1–8) in the grid, ponds were separated by <3 m. Water levels in the ponds were maintained at a depth of 30 cm by float valves.

Sixteen ponds (surface area per pond = 36.25 m²) were flooded during the period 4th August to 4th September 1987; however, conspicuous tadpole shrimp populations were found in only three ponds (F3, F5 and F6). For this study, mayfly populations in the three row F ponds were compared to three ponds (E5, E6 and E7) that lacked tadpole shrimps. In a second study, eight ponds (Ponds A1–A8: surface area per pond = 30.25 m²) were flooded during the period 29th September to 4th November 1987. Tadpole shrimps were found in six ponds.

The ponds used did not differ appreciably in several physicochemical parameters; except for the conductivity of Pond F6 (584 μMHOS cm⁻²), which was twice the size of conductivities in the other ponds. Water conductivity and pH ranged respectively from 226 to 584 μMHOS cm⁻² (mean = 276 μMHOS cm⁻²), and from 7.4 to 8.4 (mean = 7.7). The total alkalinity was similar among the ponds and averaged (±1 SD) 1.34 ± 0.13 meq l⁻¹ CaCO₃. The maximum and minimum water temperatures were measured between sampling dates with a maximum–minimum recording thermometer.

Tadpole shrimp and mayfly populations

Tadpole shrimp were sampled between 12:00 and 15:00 h with a galvanized cylindrical steel areal sampler (internal diameter = 49 cm; height = 60 cm; area = 0.189 m²). Samples were collected with a hand net (20 × 14.5 cm; mesh aperture size = 1.67 mm) following a modification of the method used by Wilbur & Travis (1984). The net was moved around the galvanized steel cylinder in circles of decreasing diameter and the cylinder was sampled until tadpole shrimps were absent from five successive samples. The total number of tadpole shrimps in each sample were counted and returned to the pond.

Ten individuals were selected randomly from each pond and carapace lengths were measured mid-dorsally to the nearest 0.5 mm on each sampling date. Because the fleshy abdominal segments can be contracted and protracted, total length measurements may vary more than those of the comparatively stiffened carapace. First instar larvae (metanaupliae) are too small (total length = 0.52–0.63 mm; Scott & Grigarick, 1979a) to be captured with the hand net; hence, only stages with a well-developed carapace were counted.

Areal samples were initially intended to investigate the spatial distribution of *T. longicaudatus* in three habitats: the corners, edges and centres of the ponds (N. S. Tietze, unpublished observations). Therefore, twelve samples per pond were taken from 4th August to 4th September. One sample was taken from each corner of the pond, and four samples were taken haphazardly along the ponds' perimeter and from the ponds' interior. The ponds were sampled four times from day 7 until day 17 after the ponds were flooded. Tadpole shrimps were not present in the ponds on day 30. The numbers of tadpole shrimps collected in the three habitats did not differ significantly using the above sampling protocol (N. S. Tietze, unpublished observations); hence, from 29th September to 4th November, five samples were taken haphazardly from each pond. The ponds were sampled twice weekly during the autumn study.

Mayflies and predacious insects were collected between 09:00 and 11:00 hours using a tow net of 19.5 cm maximum diameter and mesh openings of 153 µm. Duplicate tow net hauls were taken weekly: rows E and F, four

dates; row A, five dates. Haul lengths equalled either 6.1 m for the ponds in rows E and F or 5.5 m for the ponds in row A. Each tow net haul was preserved in the field with 95% ethanol (final concentration: 50% ethanol) and counted at 20× in the laboratory with a stereo dissecting microscope.

For the summer study, mayfly densities (number m⁻²) in ponds with and without tadpole shrimps were compared with a repeated measures ANOVA (SAS Institute, 1986). Mayfly and tadpole shrimp densities were $\log(x + 1)$ transformed prior to analysis. Because there was a continuum of tadpole shrimp densities in the autumn study, regression analyses were used to examine the relationship between mayfly density and *T. longicaudatus* density. For each date, regressions were computed using log-transformed mayfly densities and the $\log(x + 1)$ tadpole shrimp densities in the eight ponds. The effectiveness of the transformations were checked by plotting the regression residuals against the independent variable.

Headwidths of mayfly nymphs were measured as the maximum distance across the eyes. On each sampling date, mayfly headwidths were measured to the nearest 0.039 mm with an ocular micrometer to a maximum of fifty individuals from each pond. Smaller samples were used on some sampling dates for ponds with low mayfly populations. In order to compare mayfly size distributions among ponds for each sampling date, *C. californicus* nymphs were separated into seven headwidth size categories based on micrometer units. After conversion to millimeters, the size categories were: 1: 0.12–0.34 mm; 2: 0.35–0.58 mm; 3: 0.59–0.81 mm; 4: 0.82–1.02 mm; 5: 1.03–1.25 mm; 6: 1.26–1.48 mm; 7: ≥ 1.48 mm.

The distributions of headwidth size categories in some of the ponds were occasionally bimodal or skewed; therefore, for each sampling date, median headwidths were computed for every ponds. For the summer study, median mayfly headwidths in ponds with and without tadpole shrimps were compared with a repeated measures ANOVA (SAS Institute, 1986). *Triops longicaudatus* densities were $\log(x + 1)$ transformed prior to statistical analysis. The relationships between median mayfly headwidths and tadpole shrimp densities during the autumn study were determined by regression

analyses. On each date, median mayfly headwidths for the eight ponds were regressed on the $\log(x + 1)$ of *Triops* densities and regression residuals were plotted as stated above.

Associations between the abundances of mayflies, tadpole shrimps and other insect taxa

We showed previously that thirty-seven predatory taxa coexisted in the experimental ponds (Walton *et al.*, 1990b); however, for most taxa, fewer than five specimens were collected during three studies in 1987 (Walton *et al.*, 1990b). Because predators other than tadpole shrimps certainly consume mayflies, we examined the associations between *C. californicus*, *T. longicaudatus* and several insect groups. Correlations were computed for the $\log(x + 1)$ transformed abundances of anisopterans, zygopterans, dytiscid larvae, hydrophilid larvae, notonectids (adults and nymphs combined), corixids (adults and nymphs combined) vs. log-transformed *C. californicus* and *T. longicaudatus* abundances. Dytiscid adults and belostomatids were rare in tow net samples, were not associated significantly with tadpole shrimp abundance or mayfly abundance, and will not be considered further.

Laboratory studies

Apparent size-specific predation by *T. longicaudatus* was investigated in the laboratory. An individual tadpole shrimp (mean carapace length ± 1 SD ($n = 9$): 1.37 ± 0.15 cm) was placed into a plastic washtub (25.4×32 cm; water depth = 4 cm) containing 3.2 l of net filtered (mesh aperture size = $153 \mu\text{m}$) pond water. Fifteen mayfly nymphs (five per size category; mean headwidth ± 1 SD ($n = 15$): small: 0.44 ± 0.05 mm; medium: 0.83 ± 0.09 mm; large: 1.34 ± 0.08 mm) had been placed previously into the tub and were replaced as needed (every 10 min) during 1 h experiments. Individual mayflies and tadpole shrimp were used only once. Mean water temperature (± 1 SD) was $21.2 \pm 0.2^\circ\text{C}$. Predatorless controls were run concurrently and were also replicated nine times.

The escape response of *C. californicus* was measured in a 10×49.5 cm plexiglass box which was positioned over a grid of 0.5 cm squares. The water depth equalled 1 cm [net filtered

pond water (mesh aperture = $153 \mu\text{m}$)] and water temperature was 19°C . Tadpole shrimps typically contact prey with a pair of antenna-like, thoracic appendages, and in order to control the interval between stimulations and obtain visual measurements of mayfly escape responses, mayfly nymphs were gently stimulated with a minuten pin. The distances moved by mayflies of three size categories [mean headwidth ± 1 SD ($n = 12$); small: 0.37 ± 0.05 mm; medium: 0.70 ± 0.07 mm; large: 1.34 ± 0.11 mm] were measured to the nearest 0.5 cm. Five measurements were taken for each of thirty-six mayflies and a minimum of 10 s elapsed between stimulations. Only those movements along a straight path were used. The mean distance moved was calculated for each individual and the log-transformed mean distance travelled was compared among the three size classes by analysis of variance and by Tukey's HSD (Sokal & Rohlf, 1981).

Tadpole shrimp cruising speed was also measured in the plexiglass chamber. The experimental conditions were similar to those given above. Five measurements were made on each of seven tadpole shrimps (mean carinal length ± 1 SD: 1.36 ± 0.05 cm) and the average cruising speed was calculated for each tadpole shrimp.

Results

Field Study: 4th August–4th September

Tadpole shrimp populations. Tadpole shrimp populations in two ponds declined rapidly following 7 days of flooding and *Triops* had disappeared from all ponds by 1 month (Fig. 1). In Pond F6, tadpole shrimp populations did not decline appreciably until 14 days of flooding had elapsed.

During August and September, the average water temperature declined from 32.5 to 30°C (Fig. 2a) and, from day 7 to day 17 after flooding, *T. longicaudatus* size increased linearly from approximately 5 mm on day 7 to 7 mm on day 17 (Fig. 2b).

Mayfly populations. Compared with ponds without tadpole shrimps, mayfly abundance on each sampling date was significantly lower in ponds with tadpole shrimps ($F_{1,4} = 22.6$, $P < 0.01$). On average, *C. californicus* abundance in ponds with *T. longicaudatus* was twelve times lower than that in ponds without tadpole

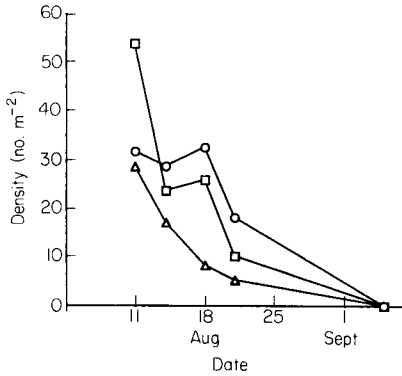


FIG. 1. Density of *Triops longicaudatus* in areal samples from 4th August until 4th September 1987: F3 (Δ), F5 (\square) and F6 (\circ).

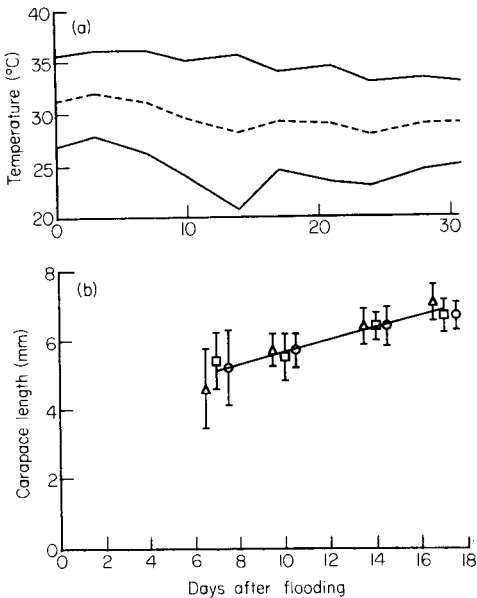


FIG. 2. Water temperature (a) and *Triops longicaudatus* carapace lengths (b) during the summer study. Maximum, minimum and average (---) water temperatures between sampling dates are illustrated. The symbols in (b) are displaced horizontally to facilitate illustration. The line in (b) is the least squares regression, carapace length (mm) = $3.84 + 0.18(\text{days})$, $r^2 = 0.92$, for the data from the three ponds: F3 (Δ), F5 (\square) and F6 (\circ).

shrimps (Fig. 3). The time by *T. longicaudatus* interaction was not significant (MANOVA; Wilks' Lambda = 2.51, $P < 0.30$).

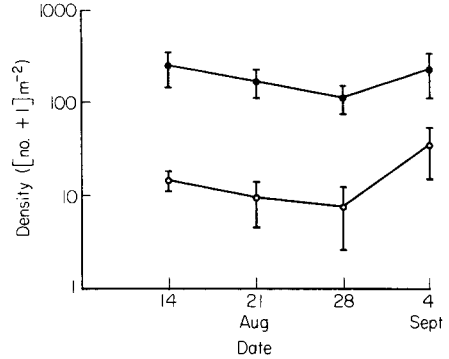


FIG. 3. Densities (± 1 SD) of *Callibaetis californicus* in ponds from 14th August until 4th September. Closed symbols = ponds without *Triops longicaudatus*. Open symbols = ponds with *T. longicaudatus*.

In addition to fewer mayfly nymphs being found in ponds with the tadpole shrimps, median mayfly headwidths differed significantly between ponds with and without *T. longicaudatus* (Fig. 4; $F_{1,3} = 11.9$, $P = 0.04$). Median mayfly headwidths increased from 14th August to 28th August in the ponds without tadpole shrimps as the first *C. californicus* cohort matured. A second cohort was evident on 4th September. The time by *T. longicaudatus* interaction was again not significant (MANOVA; Wilks' Lambda = 6.92, $P = 0.27$).

The smallest mayfly headwidth size class was absent in ponds which contained tadpole shrimps on 14 and 21 August (Fig. 4). On both dates, tadpole shrimp densities were >5 individuals m^{-2} .

Field Study: 29th September–4th November

Tadpole shrimp abundance. Tadpole shrimps were found in six of the eight ponds in row A. In five of the six ponds, *T. longicaudatus* density reached a maximum between 1 and 2 weeks after flooding and declined thereafter (Fig. 5). As observed in the first study, tadpole shrimps were found for about 1 month in most of the ponds.

The average water temperatures and *T. longicaudatus* growth rates decreased throughout the autumn study. Average water temperatures declined from approximately 28°C on 1st October to 21°C on 4th November (Fig. 6a). Whereas the average carapace lengths

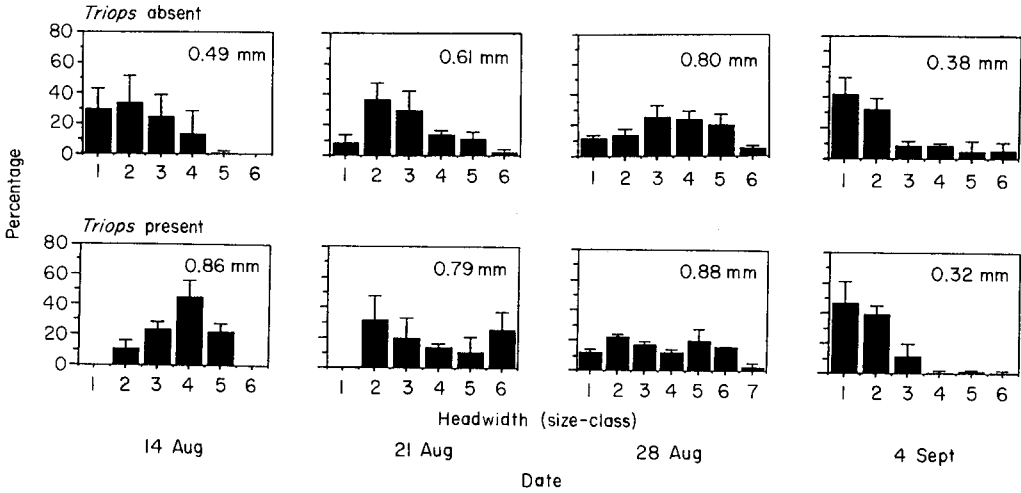


FIG. 4. The mean relative abundances (± 1 SD) and medians (mm) of *Callibaetis californicus* headwidth size classes collected from 14th August to 4th September 1987.

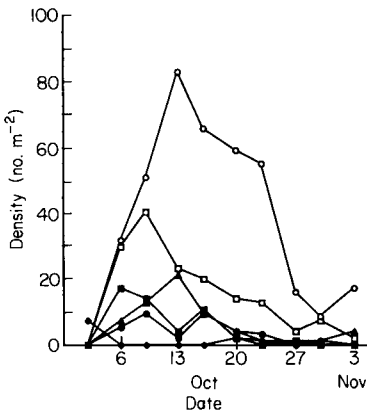


FIG. 5. Density of *Triops longicaudatus* in areal samples from 29th September to 4th November 1987: A1 (●), A2 (■), A3 (▲), A4 (◆), A6 (○) and A8 (□).

of *Triops* in Ponds A1, A2 and A3 were approximately 7.5 mm between 2 and 3 weeks after flooding (Fig. 6b), the sizes of tadpole shrimps were comparatively smaller in ponds A6 and A8 (Fig. 6c).

Pond A4 differed from the other ponds with tadpole shrimps; *T. longicaudatus* densities declined during the first week and were zero, or near zero, for the remainder of the study (Fig. 5). Water from an adjacent row seeped

into pond A4 approximately 4 days before the ponds were flooded to a depth of 30 cm. The few tadpole shrimps collected in pond A4 were larger than those collected in the other five ponds (Fig. 6b and c).

Mayfly populations. *Callibaetis californicus* abundance was negatively related to *T. longicaudatus* densities on days 21 (20 Oct.: $F_{1,6} = 17.3$, $P < 0.01$), 28 (27 Oct.: $F_{1,6} = 72.8$, $P < 0.001$) and 35 (3 Nov.: $F_{1,6} = 17.4$, $P < 0.01$) after flooding (Fig. 7). For days 21 through 35 after flooding, *Triops* density explained between 74 and 92% of the variation in mayfly abundance (Fig. 7). Mayfly abundances at 1 and 2 weeks after flooding were not significantly related to tadpole shrimp densities (Fig. 7).

Median mayfly headwidth increased directly with tadpole shrimp density on days 14 ($F_{1,6} = 15.3$, $P < 0.01$), 21 ($F_{1,6} = 6.2$, $P < 0.05$) and 28 ($F_{1,6} = 10.0$, $P < 0.001$) after flooding (Fig. 8). Tadpole shrimp density explained between 51 and 72% of the variation in mayfly size (Fig. 8). On days 7 ($F_{1,6} = 0.31$, $P > 0.05$) and 35 ($F_{1,6} = 0.05$, $P > 0.05$) after flooding, median *C. californicus* headwidths were not significantly related to *T. longicaudatus* densities (Fig. 8). Between 2 and 3 weeks after flooding, the smallest mayfly size class (13 Oct.) and size classes 1 and 2 (20 Oct.) were absent from ponds (A6 and A8) containing dense tadpole shrimp populations ($>15-20$ individuals m^{-2}).

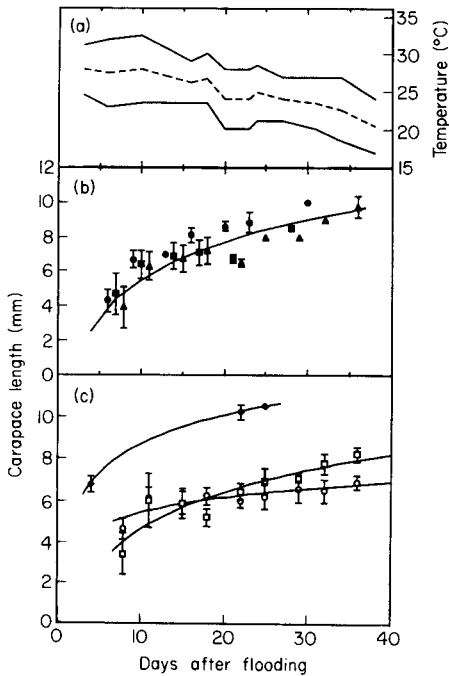


FIG. 6. Water temperature (a) and mean *Triops longicaudatus* carapace lengths (± 1 SD) (b and c) during the autumn study. Maximum, minimum and average (---) water temperatures between sampling dates are illustrated. The symbols in (b) are displaced horizontally to permit illustration. The line in (b) is the least squares regression, carapace length (c.l.: mm) = $-1.97 + 7.42[\log(\text{days})]$, $r^2 = 0.92$, for the data from A1 (\bullet), A2 (\blacksquare) and A3 (\blacktriangle). The lines in (c) are the least square regressions for each pond; A4 (\blacklozenge): c.l. = $3.98 + 4.67[\log(\text{days})]$, $r^2 = 0.99$; A6 (\circ): c.l. = $2.89 + 2.50[\log(\text{days})]$, $r^2 = 0.60$; A8 (\square): c.l. = $-1.16 + 5.77[\log(\text{days})]$, $r^2 = 0.73$.

and, on the latter date, median mayfly head-widths in ponds A6 and A8 were >1 mm.

Associations among *Triops*, *Callibaetis*, and the other insects

For most dates in both studies, *Triops* and *Callibaetis* densities were negatively correlated (Table 1). *Callibaetis californicus* abundance was either correlated directly or was not significantly associated with the abundances of other insects (Table 1). The converse was true for the associations between *T. longicaudatus* and the other insects. Heteropterans [Notonectidae: *Notonecta irrorata* Say, *N. unifasciata* Guerin

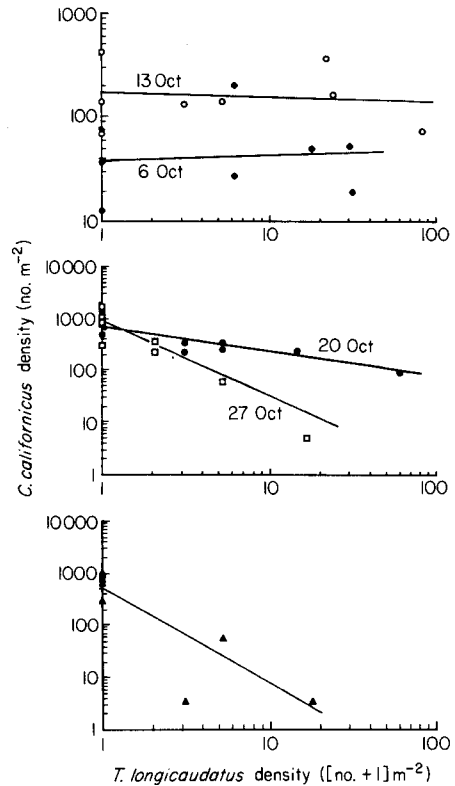


FIG. 7. Least squares regression lines for *C. californicus* density plotted against *T. longicaudatus* density on each sampling date during the autumn study. (\blacklozenge) 6 Oct.: (y) $1.60 + 0.04x$, $r^2 < 0.01$; (\circ) 13 Oct.: $y = 2.22 - 0.04x$, $r^2 = 0.01$; (\bullet) 20 Oct.: $y = 2.82 - 0.48x$, $r^2 = 0.74$; (\square) 27 Oct.: $y = 2.94 - 1.76x$, $r^2 = 0.92$; (\blacktriangle) 3 Nov.: $y = 2.72 + 1.93x$, $r^2 = 0.75$.

and *Buenoa margariacea* Bueno; Corixidae: *Corisella inscripta* (Uhler), *C. decolor* Uhler and *Trichocorixa reticulata* (Guerin)] were never significantly associated with *Triops* and, on only one date, were significantly associated with *C. californicus*. The abundances of odonates [Anisoptera: *Anax junius* (Drury), *Pantala hymanaea* (Say), *Sympetrum corruptum* (Hagen), *Tramea* spp.; Zygoptera: *Enallagma civile* (Hagen) and *Ischnura barberi* Currie] and dytiscid larvae (primarily *Laccophilus* spp.) were correlated negatively with *T. longicaudatus*, and positively with *C. californicus*, on 14th August, 20th October and 27th October.

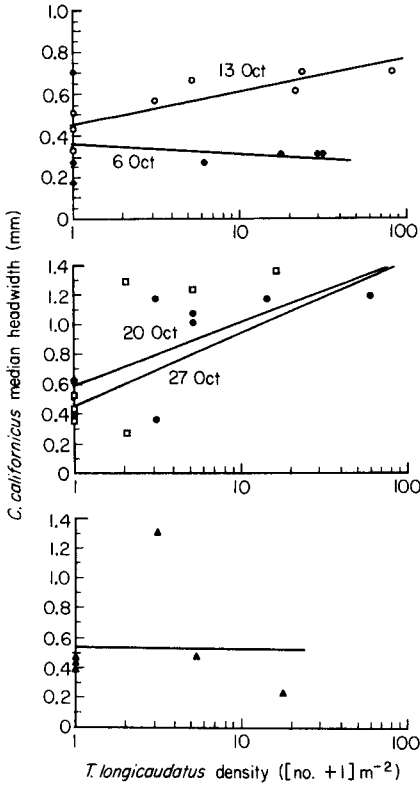


FIG. 8. Least squares regression lines for median *C. californicus* headwidth vs. *T. longicaudatus* density on each sampling date during the autumn study. (◆) 6 Oct.: $y = 0.37 - 0.05x$, $r^2 = 0.05$; (○) 13 Oct.: $y = 0.45 + 0.15x$, $r^2 = 0.72$; (●) 20 Oct.: $y = 0.59 + 0.43x$, $r^2 = 0.50$; (□) 27 Oct.: $y = 0.46 + 0.85x$, $r^2 = 0.63$; (▲) 3 Nov.: $y = 0.54 - 0.02x$, $r^2 < 0.01$.

Laboratory studies

Prey selection. When tadpole shrimps were offered three mayfly size classes in equal relative abundances, *T. longicaudatus* almost exclusively consumed the smallest mayflies. The smallest mayfly size class constituted $94 \pm 18\%$ (1 SD) of the prey captured by tadpole shrimps. Eight out of nine tadpole shrimps consumed only small mayflies and one individual consumed an equal number of small and medium mayfly nymphs. Although tadpole shrimp captured mostly small-sized individuals, on average, *T. longicaudatus* consumed only two mayflies during the 1 h observations (mean \pm 1 SD = 2 ± 1.2 prey h⁻¹).

Mayfly escape response. The distance moved

during escapes from a minuten pin differed significantly among *C. californicus* size categories ($F_{2,33} = 123.9$, $P < 0.001$) and escape distances increased significantly with nymph size (small < medium < large; Tukey's HSD, $P < 0.05$). The relationship between distance moved and headwidth was described well by a second-order polynomial:

$$y = -0.88 + 3.22x - 1.22x^2, r^2 = 0.89,$$

where y is the distance moved in log(cm) and x is headwidth in mm (Fig. 9).

Triops cruising speed. The average cruising speed of a tadpole shrimp (mean carapace length = 1.36 cm) was about 1.3 cm s^{-1} (mean \pm 1 SE: $1.26 \pm 0.59 \text{ cm s}^{-1}$). The mean cruising speed of individual tadpole shrimp ranged from 0.49 to 2.17 cm s^{-1} . During escapes, mayflies swim and then stop. As the duration of this behaviour was nearly 1 s in small mayflies, *T. longicaudatus*' cruising speeds were similar to the escape rates of small mayflies (Fig. 9). Consequently, small mayfly nymphs (i.e. headwidth size categories 1 and 2) are predicted to be more susceptible to tadpole shrimps than are large-sized mayfly nymphs.

Discussion

The abundance of *C. californicus* nymph populations is often inversely related to *T. longicaudatus* densities in small, man-made ponds. Additionally, the relative abundance of

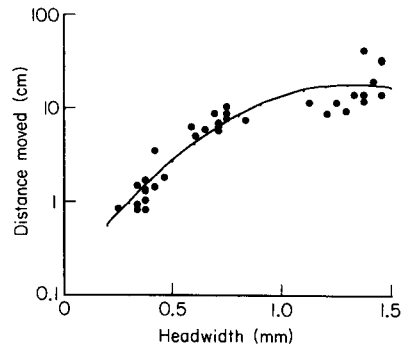


FIG. 9. The distance moved by three *Callibaetis californicus* nymph size classes during escape responses from a minuten pin. Data points are the mean distance travelled by individual nymphs.

TABLE 1. Correlations between the abundances [$\log(\text{number}+1)$] of *Callibaetis californicus*, *Triops longicaudatus* and other insects

Date	Days after flooding	<i>Callibaetis</i>	Anisoptera	Zygoptera	Dytiscid larvae	Hydrophilid larvae	Notonectids	Corixids
14 Aug.	10	<i>Callibaetis</i> -0.970***	0.948*** -0.965***	0.928*** -0.971***	0.842* -0.912***	0.993*** -0.981***	0.750 -0.740	-0.355 -0.353
21 Aug.	17	<i>Callibaetis</i> -0.956***	0.376 -0.368	0.357 -0.505	0.416 -0.503	0.693 -0.756	0.330 -0.370	-0.446 0.376
6 Oct.	7	<i>Callibaetis</i> 0.087	-0.648 -0.369	-0.190 0.028	-0.129 -0.678	-0.209 -0.451	-0.190 0.028	0.148 0.017
13 Oct.	14	<i>Callibaetis</i> -0.099	-0.067 -0.773*	-0.428 -0.635	0.162 -0.643	0.130 -0.927***	-0.532 0.414	0.198 -0.602
20 Oct.	21	<i>Callibaetis</i> -0.864**	0.802* -0.858**	0.501 -0.725*	0.907** -0.880**	0.095 0.054	0.141 0.045	0.704* -0.596
27 Oct.	28	<i>Callibaetis</i> -0.961***	0.815** -0.699*	0.826** -0.911**	0.974*** -0.935**	0.294 -0.097	0.214 -0.195	0.480 -0.378
3 Nov.	35	<i>Callibaetis</i> -0.864**	0.809* -0.755*	0.518 -0.298	-0.262 0.279	-0.526 0.554	0.675 -0.417	-0.288 0.373

* $0.05 \geq P > 0.01$;** $0.01 \geq P > 0.001$;*** $P \leq 0.001$.

small mayfly nymphs in ponds that contain tadpole shrimps was, at times, significantly less than that in ponds without *Triops*. In the laboratory, small mayfly nymphs were consumed more often by *T. longicaudatus* than were medium and large nymphs. Size-specific predation of mayfly nymphs by tadpole shrimps might explain the negative associations between *Triops* and mayfly abundances and the mayfly nymph size distributions in the Coachella Valley ponds.

During the summer study, ponds that contained tadpole shrimps were spatially segregated by row from ponds lacking *T. longicaudatus* (i.e. row E vs. F); but not by column for two of the three replicates (i.e. columns 5 and 6). The ponds in rows E and F were separated, however, by <3 m. A continuum of *T. longicaudatus* densities was found during the autumn; mayfly abundance and nymph size distributions were again associated with tadpole shrimp densities. Although these studies are not experimental, when the differences in mayfly abundances and size distributions among the ponds are considered, along with other evidence, tadpole shrimps are the most likely cause.

Differences in the physicochemical constituents of the water among the ponds were small and physicochemical factors in our Coachella Valley ponds did not limit *T. longicaudatus* or *C. californicus*; tadpole shrimps and mayflies were found in ponds at both extremes of the ranges for physicochemical factors. Bioturbation by tadpole shrimps increases water turbidity (Anonymous, 1983; Pont & Vaquer, 1986) and might depress dissolved oxygen concentrations. Compared to the physicochemical factors in our ponds, however, the physicochemical characteristics of playa lakes in New Mexico and Texas were more variable between individual lakes and were of little biological significance (Sublette & Sublette, 1967).

Tadpole shrimp population sizes and distribution in the Coachella Valley ponds are influenced more by season and historical factors than by differences in the physicochemical factors of the water. Scott & Grigarick (1979b) found that low relative humidities, low pH, high (29°C) and low (14°C) water temperatures, high salinities, and burial by sediments reduced egg hatch in *T. longicaudatus*. In the Coachella Valley ponds, tadpole shrimps were absent, or were extremely rare, from November until

February and were comparatively more abundant from May until September (Walton *et al.*, 1990a). The period between floodings and soil moisture, through its effect on the desiccation of *Triops* eggs (high soil moisture reduces egg hatch rates: L. Fry, personal communication), apparently influence the hatch success of tadpole shrimp eggs and contribute to the differences in *T. longicaudatus* population sizes between successive floodings of a particular pond. The vagaries of colonization and egg production of previous generations must also contribute respectively to the differences in tadpole shrimp populations among ponds and between floodings. Although *T. longicaudatus* was not found in ponds A5 and A7 during this study, tadpole shrimps have been observed previously (i.e. May 1986) and subsequently in both ponds (Walton *et al.* 1990a). The converse was true of *T. longicaudatus* populations in the row F ponds.

The associations among *T. longicaudatus*, *C. californicus*, and other entomofauna indicate that the negative relationship between tadpole shrimp and mayfly abundance did not result from predation on mayflies by carnivorous insects and suggest that, at times, the abundances of odonates and coleopteran larvae are also affected negatively by tadpole shrimps. The correlations of *C. californicus* abundance with predacious insect abundances were either significantly positive or non-significant. Conversely, the associations between *T. longicaudatus* and predatory insects were either significantly negative or non-significant.

Callibaetis is ovoviviparous (Edmunds *et al.*, 1976; Berner & Pescador, 1988), nymphs are recruited directly into ponds and, as evidenced by the appearance of small-sized nymphs in *Triops* ponds after the tadpole shrimps had disappeared, adult mayflies probably disperse and oviposit widely. Therefore, historical effects can be ruled out and *Callibaetis* densities in a pond at a particular time will depend on the magnitude of the *Triops* hatch. Although *C. californicus* was associated negatively with *T. longicaudatus* and either positively or non-significantly with the entomofauna, *Callibaetis hageni* (Eaton) was not significantly associated with the ceratopogonid, branchiopod (*T. longicaudatus*, anostracans and conchostracans) or notonectid-zooplankton assemblages in Utah rock pools (Dodson, 1987).

Prey-choice trials run in the laboratory showed that small mayflies (average head-width = 0.44 mm) were consumed more often by *Triops* (average carapace length = 1.37 cm) than were medium and large *C. californicus* nymphs. The distances moved during escape responses (from minuten pins) were size-related. Laboratory studies and limited observations made during the prey-selection experiments suggest that small mayflies were more susceptible to tadpole shrimps than were larger conspecifics because, after encounters with *T. longicaudatus*, small *C. californicus* nymphs moved relatively short distances and, if this movement was in the same direction as that of the predator, small nymphs were easily overtaken and captured. Previous studies also suggest that mayfly escape responses are important determinants of prey susceptibility to predators (Molles & Pietruzka, 1983; Allan *et al.*, 1987a, b).

Tietze & Mulla (1989) found that even small *T. longicaudatus* (carapace length = 2.2 mm) were carnivorous, consumed small mosquito larvae and that shrimp preference for large, fourth instar mosquito larvae increased directly with predator size. For mayflies, predation rates of relatively large tadpole shrimp were low. In laboratory studies, *T. longicaudatus* consumed approximately 2 mayflies h^{-1} at prey densities equivalent to natural densities (185 mayflies m^{-2}). Tadpole shrimps feed throughout the diel period (Scott & Grigarick, 1979a) and, if *T. longicaudatus* consumed only mayflies, this amounts to a predation rate of 48 mayfly nymphs $\text{m}^{-2} \text{day}^{-1}$ tadpole shrimp $^{-1}$. Even at low densities (i.e. 2 *Triops* m^{-2}) and in cool water (21°C), tadpole shrimps could consume more than 300 mayfly nymphs $\text{m}^{-2} \text{week}^{-1}$.

Obviously, alternative animal and plant foods, and size- and temperature-related differences in *T. longicaudatus* foraging rates must influence the impact of tadpole shrimps on mayfly populations. For example, size-related differences in tadpole shrimp foraging rates and alternative mosquito prey during the 2 weeks after flooding (Walton *et al.*, 1990b) might have been important factors which influence the temporal changes in mayfly nymph size distributions and abundances during the autumn. Mayfly size distributions differed significantly among ponds with different *T. longicaudatus* densities 1 week earlier than did mayfly abun-

dance. In the autumn, it may take several weeks before *T. longicaudatus* detectably reduces the mayfly populations which recruit during the first week after flooding and continue recruitment thereafter. As compared to the autumnal study, warmer water, greater tadpole shrimp foraging rates, lower densities of alternative culicine prey (Walton *et al.*, 1990b), and smaller mayfly populations in the summer may explain why mayfly abundances and size distributions in ponds, with and without *T. longicaudatus*, differed earlier and at lower tadpole shrimp densities (>5 vs. 15–20 tadpole shrimps m^{-2}).

Previous studies found that *Triops* spp. densities were often greater than 100 individuals per square metre but the effects of tadpole shrimps on the co-occurring entomofauna were not described. Barthelmes (1963) reported that tadpole shrimp densities in fish ponds were between 20 and 266 individuals per square metre. In rice fields, *T. cancriformis* densities reached 300 individuals per square metre; however, tadpole shrimp densities differed among sampling stations, ranged generally between 13 and 180 individuals per square metre, and populations declined to zero after 1 month (Pont & Vaquer, 1986). In our study, *T. longicaudatus* densities were less than 100 individuals per square metre, tadpole shrimp populations also persisted for nearly 1 month, and the negative associations between *T. longicaudatus* and *C. californicus* were evident at comparatively low tadpole shrimp densities.

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