

# LARVAL POPULATION DYNAMICS IN A COMMUNITY OF NEARCTIC *Aedes* INHABITING A TEMPORARY VERNAL POOL

AMY MORRISON<sup>1</sup> AND THEODORE G. ANDREADIS<sup>2</sup>

**ABSTRACT.** The spatial distribution and preadult mortality patterns of 4 cohabiting species of *Aedes* mosquitoes were studied in a temporary vernal pool at Mt. Carmel, CT, from March to May 1990. The dominant species was *Ae. stimulans* (79.9%), followed by *Ae. canadensis* (10.7%), *Ae. excrucians* (7.5%) and *Ae. cinereus* (1.9%). First instar larvae of all species aggregated at the edge of the pool and then dispersed to deeper regions as they matured. Larval mortality was high, and the majority occurred during the first stadium (80.9% for *Ae. canadensis*, 88.9% for *Ae. excrucians*, 89.1% for *Ae. stimulans* and 90.0% for *Ae. cinereus*). A predatory chaobrid, *Mochlonyx cinctipes*, was implicated as the major mortality factor affecting larval populations.

## INTRODUCTION

A comprehensive understanding of larval mosquito population dynamics can facilitate the development of more effective and appropriate control strategies. This is particularly important with biological agents (e.g., parasites and predators), because these organisms, unlike insecticides, are greatly influenced by density-dependent processes that operate on larval populations (Service 1985a, 1985b, 1989).

Unfortunately, there is very little information on natural pre-adult mortality for most species of mosquitoes. In those studies that have been conducted (see Barr 1985 and Service 1985a for reviews), such mortality has typically been high (> 80%) and has generally been attributed to intraspecific larval competition for limited resources, most notably food, and to a lesser degree, to predation. However, most studies have focused on single species. Few have examined interactions among cohabiting species in the same natural habitat.

Temporary vernal pools, commonly referred to as snowmelt pools, are unique habitats that serve as important production sites for many species of Nearctic *Aedes*, most of which are univoltine (Wiggins et al. 1980, Laird 1988). Pools are formed in the early spring (during March in Connecticut) from melting snow and rain, gradually dry by early June, and remain so until the following spring. These sites are typically inhabited by several species of *Aedes* which coexist and apparently compete with one another. The various factors affecting the structure of these larval communities and their population dynamics have not been previously examined.

This study explores larval ecology and population dynamics in a temporary vernal pool inhabited by *Aedes canadensis canadensis* (Theobald), *Aedes cinereus* Meigen, *Aedes excrucians* (Walker) and *Aedes stimulans* (Walker) in an attempt to determine the spatial and temporal distribution of each species, preadult mortality patterns, and the impact of natural enemies and limiting abiotic factors (rainfall and water levels) on the larval community.

## MATERIALS AND METHODS

**Study site:** The study was conducted in a temporary, leaf-lined, vernal pool (approximately 15 × 6 m, maximum depth = 76.5 cm) located in an isolated woodland habitat dominated by white pine, *Pinus strobi*, and eastern hemlock, *Tsuga canadensis*, in Mt. Carmel, Connecticut. The pool was selected for study because: 1) it is the only site where mosquito larvae have been found in this woodlot; 2) it habitually supports larval populations of *Ae. canadensis*, *Ae. cinereus*, *Ae. excrucians* and *Ae. stimulans* which hatch in early March and emerge by mid-May; and 3) it is usually dry from June through February (T. G. Andreadis, unpublished data).

The dimensions (length, width at center and depth) of the pool were measured weekly and the surface area was calculated. Water temperatures were monitored using a standard maximum/minimum thermometer. Precipitation data were obtained from an official National Weather Service Climatological Station that was located less than 1.6 km away.

**Sampling methodology:** The pool was monitored twice weekly in early March for ice melt and sampling was initiated with the onset of egg hatch (March 15, 1990). Larval collections were then made weekly (from 0900–1100 h) until the end of adult emergence (May 10). Sample points were established as follows. Stakes were placed at 10 equidistant points around the periphery of the pool (Fig. 1). These points marked a transect extending from the 30.6 to 91.8 cm depth range up to the edge. Four samples, using a standard

<sup>1</sup> Yale Arbovirus Research Unit, Department of Epidemiology and Public Health, Yale University School of Medicine, P.O. Box 3333, New Haven, CT 06510.

<sup>2</sup> Department of Entomology, The Connecticut Agricultural Experiment Station, P.O. Box 1106, New Haven, CT 06504.

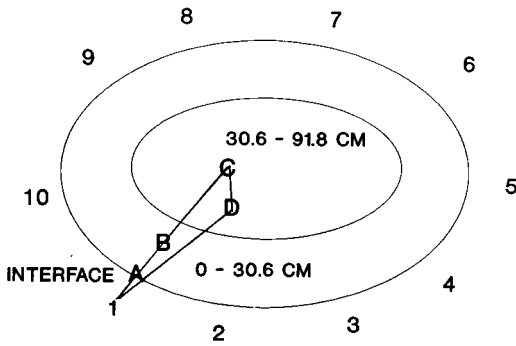


Fig. 1. Schematic diagram of the study pool showing the location of the four sample points (A-D) along the transect lines (1-10) in each of the three depth zones (interface, 0-30.6 cm, 30.6-91.8 cm).

350 ml mosquito dipper, were consecutively taken at each of the 10 points in the following order: 1) the edge (interface), 2) the 0-30.6 cm depth range, 3) the surface, and 4) bottom of the 30.6-91.8 cm depth range. The time interval between samples was 2-3 min and all sampling was completed within 2 hours. Each sample ( $n = 40$ ) was individually placed in a 500 ml plastic bag and immediately transferred to the laboratory. Based on 4 years of extensive sampling in this pool using various techniques (Andreadis 1985), we did not consider the current sampling methodology to be a significant mortality factor.

**Identification of field material:** All field material was sorted and examined on the date of collection. Mosquito species were identified and the total number of each instar found was recorded for each of the 40 samples. Instars were identified according to Means (1979). First instar larvae that were not readily identifiable, were reared to the second stadium and then identified and counted. Pupae were isolated in individual vials, allowed to emerge and identified as adults. All potential predators (chaoborids and cyclopoid copepods) were identified and quantified in a similar manner. The data were recorded by date and sample point.

**Statistical analysis:** Because of the pool's uneven bottom and variable shape, no attempt was made to calculate the total number of individuals within the pool. However, since the sampling procedure was standardized (40 dips each week at identical sites), the relative abundance of each of the various organisms could be determined for each sample date. The data did not conform to normality and therefore non-parametric tests were selected for analyses. Mann-Whitney U tests were used to quantify changes in larval mosquito and predator densities over time. Spatial and temporal distribution of mosquito instar, species, and predator populations

were verified using Kruskal-Wallis tests for each sample date and the entire study period. Tests were either calculated by hand or by using the SAS Institute (1985) program PROC NPAR1WAY WILCOXON. Spearman correlation analysis was performed on the following variables: sample date; mosquito, chaobrid and copepod density; and water level. The SAS program PROC SPEARMAN was used to calculate Spearman coefficients and their respective  $P$ -values. Probabilities of 5% or less were considered significant.

## RESULTS

**Pool fluctuations and climatological data:** The surface area of the pool increased from 50.5 m<sup>2</sup> on March 15 to a maximum of 91.8 m<sup>2</sup> on April 5, and then gradually receded to its original level (56.4 m<sup>2</sup>) by the end of adult emergence (May 10) (Fig. 2). These fluctuations corresponded with weekly measurements of rainfall which totaled 22.7 cm for the same period. Water temperatures ranged from 4 to 18°C and averaged ( $\pm$  SD) 9.0  $\pm$  1.5°C in March, 9.1  $\pm$  1.6°C in April, and 13.2  $\pm$  1.8°C in May.

**Larval mosquito density estimates:** The weekly relative abundance of all immature stages of each of the 4 mosquito species found inhabiting the pool during the 8-wk sampling period is shown (Fig. 3). The most abundant species overall was *Ae. stimulans* (79.9%) ( $n = 1,144$ ) followed by *Ae. canadensis* (10.7%), *Ae. excrucians* (7.5%) and *Ae. cinereus* (1.9%).

Egg hatch of *Ae. stimulans*, *Ae. canadensis* and *Ae. excrucians* was first detected on March 15. The most predominant species was *Ae. stimulans*. A significant ( $P < 0.01$ ; Mann-Whitney

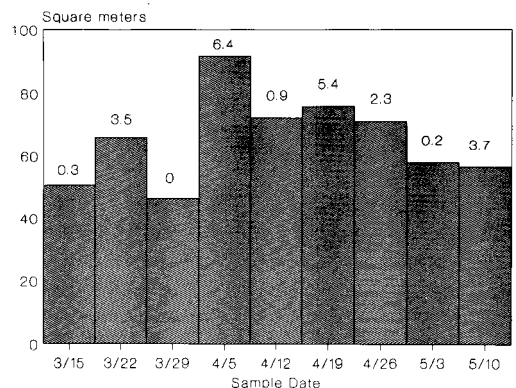


Fig. 2. Weekly measurements of pool surface area from March 15 to May 10. Numbers above each column indicate rainfall amounts (cm) for each sampling period.

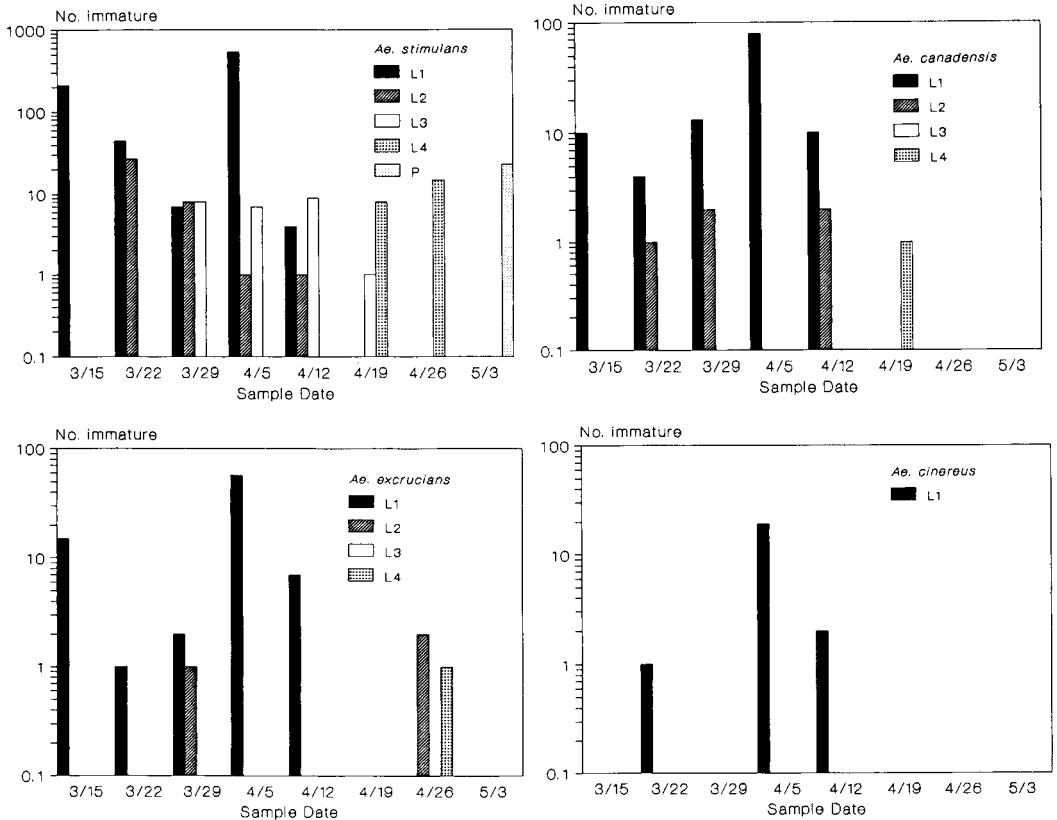


Fig. 3. Weekly relative abundance of immature *Aedes canadensis*, *Aedes cinereus*, *Aedes excrucians* and *Aedes stimulans* developing within the study pool at Mt. Carmel, CT, from March 15 to May 3, 1990. (L1-L4 = larval instars, P = pupae).

U test) decline in *Ae. stimulans* was observed during the second week (March 22). Fewer numbers of *Ae. canadensis* and *Ae. excrucians* were also collected at this time, but these reductions were not significant ( $P > 0.1$ ; Mann-Whitney U test). A single *Aedes cinereus* larva was found on this sampling date as well.

Small increases in the number of *Ae. canadensis* and *Ae. excrucians* were seen on March 29. However, populations of *Ae. stimulans* continued to decline ( $P < 0.1$ ; Mann-Whitney U test). While equal numbers of first through third instar *Ae. stimulans* were observed, first instars were still the most common stage found in populations of *Ae. canadensis* and *Ae. excrucians*.

A large increase in the population densities of all 4 species was observed on April 5. These increases followed a week of heavy rainfall (6.4 cm) which raised water levels in the pool (Fig. 2) and thus stimulated a second major hatch, as evidenced by the large numbers of first instar larvae (98.9% of total larvae collected).

An equally marked decline in the relative abundance of all species ( $P < 0.02$  for each species) was seen during the following week (April 12). This group was still mostly first instars but some second instar *Ae. canadensis* and third instar *Ae. stimulans* were also collected.

Population levels of *Ae. stimulans* stabilized during weeks 6-8 (April 19 through May 3), and the maturation of all remaining larvae was consistently uniform right through to pupation and adult emergence. The abundance of each of the other 3 species, however, abruptly declined and no larvae or pupae of *Ae. cinereus*, *Ae. canadensis* or *Ae. excrucians* were found after April 12, 19 and 26, respectively.

**Spatial distribution:** Clear patterns of larval aggregation were observed among different instars at various depths within the pool (Table 1). First instar larvae of all 4 mosquito species were consistently found along the water's edge on each sample date that they were present ( $P$

< 0.0001 for *Ae. stimulans* and  $P < 0.0002$  for *Ae. canadensis*, *Ae. cinereus* and *Ae. excrucians*, Kruskal-Wallis tests). There was no consistent aggregation of second instars, however, as comparable numbers were found at the interface, 0–30.6 cm and 30.6–91.8 cm (surface) depth ranges. Third and fourth instar larvae were concentrated in the deeper portions of the pool while pupae were generally found along the interface and surface.

**Impact of potential predators:** One species of Chaoboridae, *Mochlonyx cinctipes* (Coq.) and 3 species of cyclopoid copepods (*Acanthocyclops vernalis* (Fisher), *Cyclops venustoides* Cocker and *Orthocyclops modestus* (Herrick)) were found in the pool. The relative abundance of these organisms from March 15 through May 10 is summarized (Fig. 4). *Mochlonyx cinctipes* was detected on the same date that mosquito hatch was observed (March 15). Populations decreased slightly for 3 consecutive weeks but then increased 3.5× on April 12, one week following the increase in the water level of the pool (Fig. 2). These populations exhibited a gradual but insignificant ( $P > 0.1$ , Mann-Whitney U test) decline in subsequent weeks. Adult copepod populations were also detected on March 15 but, with the exception of a small increase on March 29, steadily decreased over time until they were virtually absent. An analysis of distribution data showed a significant aggregation of *M. cinctipes* and all copepod species along the edge of the pool (Table 1).

The only other natural enemy observed was a microsporidian (*Amblyospora* sp.), which was found infecting < 1% of all field-collected *Ae. stimulans* larvae, and thus did not appear to be a significant mortality factor.

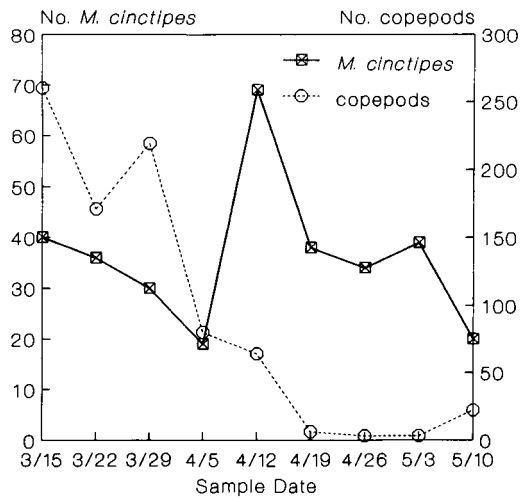


Fig. 4. Weekly relative abundance of immature *Mochlonyx cinctipes* and adult female copepods (*Acanthocyclops vernalis*, *Cyclops venustoides* and *Orthocyclops modestus*) found within the study pool at Mt. Carmel, CT, from March 15 to May 10, 1990.

DISCUSSION

Four species of mosquitoes were found to co-habit the temporary vernal pool examined in this study. The most abundant species was *Ae. stimulans* followed by *Ae. canadensis*, *Ae. excrucians* and *Ae. cinereus*. Two distinct periods of egg hatch were observed. The first was detected on March 15 and included hatch of all species except *Ae. cinereus*. This suggests that at least some overwintered eggs of *Ae. stimulans*, *Ae. canadensis* and *Ae. excrucians* respond to the same early hatching stimuli. Our findings are

Table 1. Mean (±SD) number immature mosquitoes (*Aedes canadensis*, *Aedes cinereus*, *Aedes excrucians* and *Aedes stimulans*), larval *Mochlonyx cinctipes*, and adult female copepods (*Acanthocyclops vernalis*, *Cyclops venustoides* and *Orthocyclops modestus*) collected at various sample depths from March 15 to May 10, 1990 at Mt. Carmel, CT.

Group and stage	n	Pool depth				P	Weeks present
		Interface	0–30.6 cm	30.6–91.8 cm			
				Surface	Bottom		
Immature mosquitoes							
L1	50	18.3 ± 38.3	1.8 ± 6.4	0.4 ± 0.9	0.1 ± 0.3	0.0001	(1*, 2*, 3*, 4*, 5*)
L2	50	0.2 ± 0.5	0.4 ± 0.8	0.3 ± 0.3	0.1 ± 0.2	0.067	(2*, 3, 4, 5, 7)
L3	40	0	0.1 ± 0.4	0.3 ± 0.6	0.1 ± 0.5	0.003	(3, 4*, 5*, 6)
L4	20	0	0.3 ± 0.4	0.6 ± 0.5	0.5 ± 0.7	0.002	(6, 7*)
P	10	1.1 ± 1.3	0.2 ± 0.4	1.0 ± 0.8	0	0.003	(8*)
<i>M. cinctipes</i>	90	2.3 ± 2.6	0.6 ± 0.9	0.3 ± 0.5	0.5 ± 0.8	0.0001	(1, 2*, 3, 4, 5, 6*, 7*, 8*, 9)
Copepods	90	7.5 ± 12.1	0.9 ± 2.7	0.4 ± 1.8	0.4 ± 0.9	0.0001	(1*, 2*, 3*, 4*, 5*, 6, 7, 8, 9*)

\*  $P < 0.05$ .

also consistent with other reports that these 3 species are often the first to appear in snowmelt pools (Means 1979) while *Ae. cinereus* is one of the last to hatch in the spring (Happold 1965). The small increases in the abundance of *Ae. canadensis* observed from March 15–29 in the absence of any additional flooding, further imply that egg hatch for this species may be more irregular than *Ae. stimulans* as has been noted by others (Breeland et al. 1961).

The second major hatch occurred 3 wk after initial egg hatch and coincided with a 45 m<sup>2</sup> increase in the surface area of the pool, which presumably resulted in the inundation of additional eggs. The larger proportion of *Ae. canadensis*, *Ae. excrucians* and *Ae. cinereus* observed during this second hatch indicate that these mosquitoes may lay their eggs at higher strata levels of the depression than *Ae. stimulans*.

The spatial distribution data show that first instar larvae of all 4 mosquito species congregate in the shallows at the edge of the pool. As these larvae mature, however, they appear to disperse outward toward deeper regions and in the case of *Ae. stimulans*, return to the edge of the pool only at the time of pupation. The reasons for this behavior are unknown but could possibly be a response to horizontal and/or vertical temperature gradients in the pool or changes in light intensity, as has been documented for *Aedes communis* (De Geer) (Haufe 1957).

Our data indicate that larval mortality was high among all 4 mosquito species and that the majority of this mortality occurred during the first stadium. Estimates of actual larval mortality were difficult to determine due to asynchronous hatch of larvae and the additional flooding that resulted in a second major egg hatch observed on April 5. However, conservative estimates of first instar mortality for each species could be calculated based on population changes from March 15 to 22 (March 22 to 29 for *Ae. cinereus*) and April 5 to 12. Estimated first instar mortality was 80.9% for *Ae. canadensis*, 88.9% for *Ae. excrucians*, 89.1% for *Ae. stimulans* and 90.0% for *Ae. cinereus*. The greatest amount of this mortality was associated with the second major hatch in April (94.9% vs. 66.2% in March). These levels of larval mortality are consistent with estimates of preadult mortality in other *Aedes* mosquitoes that develop in shallow temporary pools including *Aedes cantans* (Meigen) (90–94%) (Lakhani and Service 1974, Service 1977), *Aedes cantator* (Coq.) (96%) (Andreadis 1989), *Ae. communis* (87%) (Iversen 1971) and *Aedes euedes* Howard, Dyar and Knab and *Aedes mercurator* Dyar (>90%) (Enfield and Pritchard 1977).

*Aedes stimulans* was the only species that pupated. Although we cannot rule out possible bias in our sampling methodology that may have prevented us from detecting the pupation of other species, especially because their population densities were considerably lower, this observation further establishes *Ae. stimulans* as the most successful mosquito species in this habitat.

According to Service (1985a), mosquito populations are usually regulated by density-dependent processes. These processes include larval competition for limited resources (mostly food), predation and parasitism. We infer that larval competition for food may be less important than predation in this habitat. Although we did not measure food reserves within the pool, Barlocher et al. (1978) and Wiggins et al. (1980) have demonstrated that temporary vernal pools have high protein levels and rich food resources that are available to detritivores such as mosquito larvae. According to Wiggins et al. (1980), this results from rapid aerobic decomposition with the annual flooding in the spring that releases a pulse of nutrients. This observation combined with the consistently high level of water that was maintained within the pool up until the onset of adult emergence, would therefore, appear to deemphasize larval overcrowding and lack of food as significant mortality factors.

The distribution and abundance of *M. cinctipes* within the pool from March through May would seem to implicate this predaceous chaobrid. *Mochlonyx cinctipes* is a well known predator of mosquito larvae (Twinn 1926, 1931; Haufe 1952, O'Conner 1959) which can consume an average of 1.4 larvae/day (Twinn 1931). It is commonly found within the shallow margins of semipermanent woodland pools (O'Conner 1959) and may cause marked reductions in larval populations of several species of spring *Aedes* including *Ae. canadensis*, *Ae. cinereus*, *Ae. excrucians*, *Ae. stimulans*, *Aedes fitchii* (Felt and Young), *Aedes sticticus* (Meigen) and *Aedes vexans* (Meigen) (Twinn 1926, 1931; Haufe 1952). Based on the large numbers of *M. cinctipes* found associated with early instar mosquito larvae along the interface of the pool, conspicuous absence of other significant larval pathogens or predators, and stable water levels, it appears that *M. cinctipes* may have played a major role in reducing larval densities in this temporary vernal pool, especially after the second major larval hatch in April when populations of *M. cinctipes* were at their highest, and first instar larval mortality was greatest.

The role of cyclopoid copepods is less apparent. With the exception of *A. vernalis* (Marten 1990), the larvivorous tendencies of the other 2

species found breeding in the pool are unknown. However, based on the comparatively low numbers observed in early April when most larval mortality was occurring, it appears that their impact on the population was considerably less.

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