MORTALITY AND SURVIVAL PATTERNS FOR THE IMMATURE STAGES OF *PSOROPHORA COLUMBIAE*[1]

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ABSTRACT. To determine the patterns of *Psorophora columbiae* survival and mortality, methods were employed that involved the simultaneous use of laboratory-reared cohorts, predator-exclusion cages, and field estimates of larval dynamics. Laboratory studies indicated that the maximum daily survival averaged from 0.92 for day-old larvae to 1.0 for the older age classes with no significant differences (P>0.05) in survival among days. Data from predator-exclusion cages indicated that mortality inflicted by factors other than predation was significantly (P<0.05) more intense in the younger age classes and the relatively few individuals that survived to the older age classes had a high expectation of successful emergence. A quantitative estimate of the mortality inflicted on *Ps. columbiae* larvae by all indigenous natural enemies indicated that mortality rates were higher in the older age classes. This supports the view that the predator complex is a major source of irreplaceable mortality for immature mosquitoes inhabiting Louisiana rice fields.

INTRODUCTION

The development of an integrated approach to riceland mosquito management requires the ability to forecast when and where adult mosquito populations will reach injurious or noxious levels. Since adult population levels are influenced by their survival as immatures, the prediction of adult emergence patterns presupposes that rates of larval mortality may be predicted. Information regarding the survival rates of riceland mosquito larvae has not been available, although it is generally accepted that few organisms die of senescence. Most organisms succumb to parasites, pathogens and other hazards before they reach old age (Krebs 1972). However, it is sometimes assumed for the construction of demographic models that larval mortality rates are independent of age. The construction of dynamic models of larval mortality is essential to plan the most effective riceland mosquito control techniques, the development of new techniques and the integration of technologies into pest management schemes.

The present research differs from previous survivorship studies in that the methods of collecting, interpreting and utilizing data that pertain specifically to the dynamics and management of immature riceland mosquito populations in Louisiana have been adequately described. Acceptable survey techniques and the methods of data analyses, which will enable the precise estimation of larval density, have been developed (Andis et al. 1983, Andis and Meek 1984). However, at present, the number of larvae cannot be related to the total number of adults, much less the number of females that will emerge. Consequently, the objectives of this study were: 1) to establish patterns of larval mortality and survival under laboratory conditions in which many individuals may survive to die of old age; they therefore represent the baseline state that is modified on exposure to natural conditions; 2) to estimate the maximum larval survival rate under field conditions by eliminating the mortality inflicted by indigenous natural enemies, and 3) to quantify total prey mortality, which would provide an estimate of the number of adults expected to emerge from a known larval density.

METHODS AND MATERIALS

To obtain the information required to discern patterns of *Psorophora columbiae* (Dyar and Knab) survival and mortality, methods were employed that involved the simultaneous use of laboratory-reared cohorts, predator-exclusion cages, and field estimates of larval dynamics. These methods estimated the maximum survival under optimum environmental conditions, the mortality inflicted by factors other than predation, and the total mortality, respectively. A quantitative estimate of the mortality inflicted on *Ps. columbiae* larvae by all indigenous natural enemies was obtained by subtracting non-predator induced mortality from total mortality. Field studies were conducted during 1983 and 1984 in 18 and 21-ha commercial rice fields, respectively, located in Vermilion Parish, LA. Eggs used in all studies were

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obtained from field-collected *Ps. columbiae* females in Vermilion Parish, subsequently stored in the laboratory, and hatched using methods described by McHugh and Olson (1982). Only the larvae that hatched during the first 2 hr were used in the tests to ensure that all experiments were initiated with larvae approximately the same age.

Survival data were transformed and subjected to analyses of variance using SAS general linear models procedure for testing the hypothesis that the mean survival rates were equal (SAS 1983). Following rejection of this hypothesis, a Newman-Keuls multiple-range test was used to test for differences in survival among larval ages.

Laboratory survival. Fifty larvae were placed in each of 12 enameled pans (18 × 30 cm) filled with ca. 1 liter of deionized water stabilized at 34°C. The larval pans were placed in an environmental chamber and maintained at 34±0.5°C under a 14:10 light:dark cycle until emergence was completed. Larvae were fed a 1:1:1 mixture of brewer's yeast, lactalbumin and ground rodent chow as described by McHugh and Olson (1982). Larvae were counted daily and survival rates, expressed as the probability of a larva surviving the next 24 hr, were calculated. Upon pupation, the pupae were transferred to styrene emergence containers and the emerged adults were counted and sexed. This procedure was repeated for each set of the 13 field tests conducted.

Survival under predator-free conditions. Predator-exclusion cages were constructed of polyvinylchloride pipe (32 cm high × 38.1 cm diam) that provided an effective larval habitat of 0.11 m² (Fig. 1). Holes (6.35 cm diam) were drilled along the sides to allow water to flow through the cage and covered with 50-mesh Saran[3] screen, as was the bottom.

Based on previously reported data regarding the spatial patterns of *Ps. columbiae* larvae (Andis and Meek 1984), 7 cages/field were placed within 1 m of the earthen levees prior to harvest and at random locations within the pans (areas between the earthen levees) following harvest. Each cage was stocked with 100 larvae, which resulted in an initial density comparable with that used in the laboratory studies and within the densities of natural populations (Chambers et al. 1979, Andis et al. 1983). These cages were kept free of predators by a screen covering and the numbers of larvae and pupae recorded daily. Upon the initiation of pupation, the screen covering was replaced by a funnel

constructed of plastic laminated window screen (16 mesh) and a modified mosquito breeder[4] (Fig. 1) which collected the emerged adults and allowed them to be counted and sexed. Due to the daily disruption of the predator-exclusion cages, 3 additional cages were placed in each field and monitored only for adult emergence. Data from the cages monitored for survival and emergence were subjected to paired-*t* analyses for testing the hypothesis that mean emergence from both sets of cages was equal and thus that adult emergence was unaffected by the daily disruptions of the larval survival cages. Additionally, selected physiochemical parameters, viz. temperature, dissolved oxygen, salinity and conductivity of the water, were monitored daily inside the survival cages as well as in the rice field to ensure that the cages themselves were not responsible for any added mortality.

Predator exclusion enabled the calculation of maximum field survival rates and provided insight into the factors, other than predation, that cause population change. In addition, baseline data were established on the maximum number of *Ps. columbiae* females expected to emerge from a known larval density under field conditions.

Survival of natural populations. Estimates of total daily survival were obtained by larval sampling following the procedures described by Andis et al. (1983) and Andis and Meek (1984). Due to the unusually low abundance of natural *Ps. columbiae* populations, dipper samples were obtained daily for each rice field during only one of the predator exclusion experiments described above.

Statistical analyses were based on a model utilizing 2 fields with 3 pans/field, 15 replicates/pan, one dipper sample consisting of 10 dips/replication for a total of 450 dips collected/field/day. The numbers of larvae/0.1 m² were estimated from mean dipper values (Andis et al. 1983) and daily comparisons made. Losses due to dispersal among pans were considered negligible.

RESULTS AND DISCUSSION

Laboratory survival. Under laboratory conditions, the maximum daily survival of *Ps. columbiae* larvae averaged 0.92 for the younger age classes up to 1.0 for the older (Table 1). There were no significant differences in survival (P>0.05) among larval ages or dates; the average adult emergence rate was 88.3% with a male:female ratio of 1.08:0.92. These data rep-
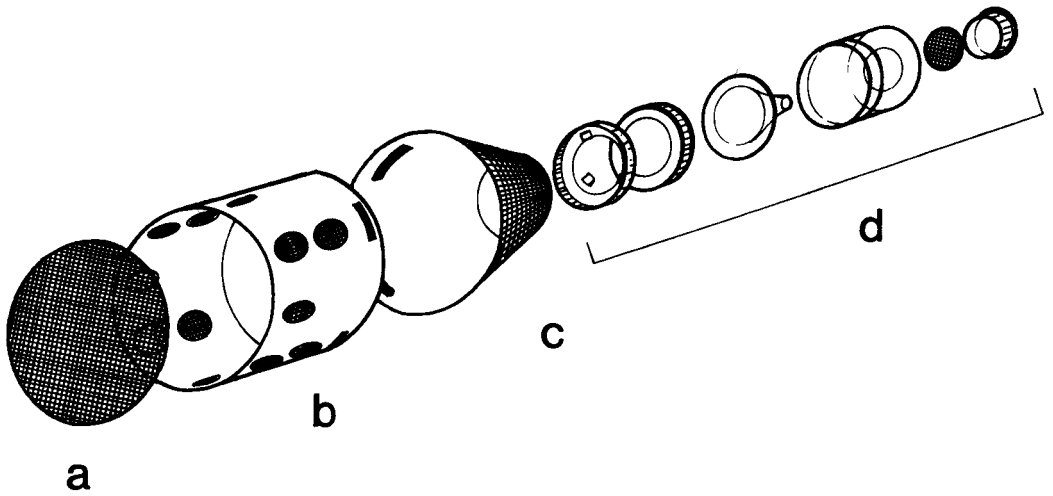
Fig. 1. Schematic view of predator-exclusion cage. A. Saran screen bottom, B. Polyvinylchloride tube, C. Funnel, D. Modified mosquito breeder.

resent the baseline values that were modified upon exposure to field conditions. Investigation of the possible effect of intraspecific competition indicated that a 3-fold increase in larval density did not significantly affect (P>0.05) survival of *Ps. columbiae* larvae. This increased density was well above that encountered in natural rice field populations and indicates that intraspecific competition may not be an important factor limiting larval survival or adult emergence of *Ps. columbiae* populations.

SURVIVAL UNDER PREDATOR-FREE CONDITIONS. The maximum daily survival rates under predator-free field conditions were significantly less (P<0.05) than the laboratory survival rates. The predator-free survival rates increased with larval development, averaging 0.86 for the younger age classes up to 0.98 for the older (Table 2). A graphic record of these data was obtained by plotting the number of survivors against time (Fig. 2). On all dates, the survivorship curves plotted for each field were posi-
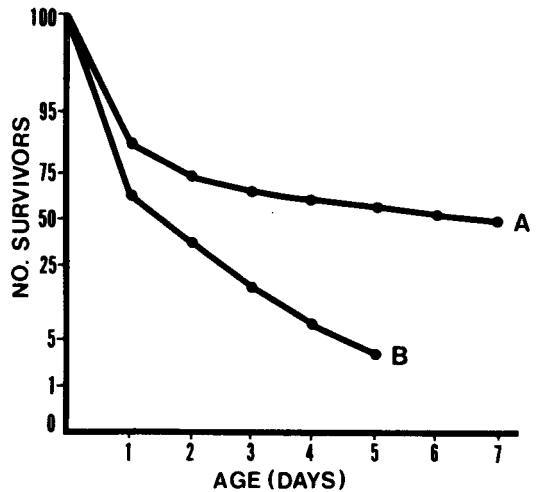

Fig. 2. Survivorship curves of *Ps. columbiae* larvae in rice fields. A. under predator-free conditions. B. in the presence of predators.

Table 1. Mean daily survival rates for *Psorophora columbiae* larvae reared under laboratory conditions.*

| Age (days) | 1983 | | | | | | | | 1984 | | | | | |
| | August | | | | Sept. | | | | July | August | | | Sept. | |
	5	12	18	26	1	8	15	22	5	3	17	31	7	Mean**
1	0.90	0.89	0.94	0.90	0.91	0.92	0.92	0.93	0.87	0.94	0.92	0.92	0.93	0.92a
2	0.94	0.97	0.96	0.93	0.95	0.97	0.97	0.98	0.96	0.96	0.96	0.95	0.94	0.96a
3	1.00	1.00	1.00	0.99	1.00	1.00	0.99	1.00	1.00	1.00	0.98	1.00	1.00	1.00a
4	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	0.98	1.00	1.00a
5	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00a
6	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00a

* Expressed as the probability of a larva surviving the next 24 hr.
** Means followed by the same letter are not significantly different (P>0.05).

Table 2. Mean daily survival rates for *Psorophora columbiae* larvae reared in predator-exclusion cages in Louisiana rice fields.*

| Age (days) | 1983 | | | | | | | | 1984 | | | | | Mean** |
| | August | | | | Sept. | | | | July | August | | | Sept. | |
	5	12	18	26	1	8	15	22	5	3	17	31	7	
1	0.83	0.86	0.82	0.84	0.93	0.88	0.83	0.85	0.80	0.84	0.87	0.93	0.89	0.86a
2	0.83	0.86	0.82	0.84	0.93	0.88	0.83	0.85	0.80	0.84	0.87	0.93	0.89	0.86a
3	0.83	0.86	0.82	0.84	0.93	0.88	0.83	0.85	0.80	0.84	0.87	0.93	0.89	0.86a
4	0.84	0.89	0.84	0.86	0.95	0.91	0.89	0.84	0.84	0.88	0.89	0.96	0.94	0.89a
5	0.92	0.89	0.90	0.90	0.99	0.97	0.90	0.91	0.91	0.92	0.93	0.99	0.98	0.93b
6	0.97	0.91	0.97	0.94	1.00	0.99	0.92	0.94	0.94	0.95	0.95	0.97	1.00	0.96b
7	0.97	0.99	0.99	0.99	—	—	0.98	0.99	0.97	0.99	0.99	—	—	0.98b

* Expressed as the probability of a larva surviving the next 24 hr.
** Means followed by the same letter are not significantly different ($P>0.05$).

tively skewed, indicating mortality, when predators were excluded, was significantly more intense ($P<0.05$) in the younger age classes and the relatively few individuals that survived to the older age classes had a high expectation of successful emergence.

There was no clear trend of association between survival and season. However, the significant increases ($P<0.05$) in the daily survival rates of the younger age classes immediately following harvests (September 1, 1983 and August 31, 1984) should be noted (Table 2). It is apparent, from the adult emergence data, that these increases in post-harvest survival were important to the dynamics of the *Ps. columbiae* populations and resulted in a highly significant increase ($P<0.01$) in the proportion of adults emerging (Table 3). Williams et al. (1983) established that no association existed between the number of eggs and adult population size over time. These observations, in conjunction with the previous data, suggest that the fluctuation of adult *Ps. columbiae* populations may de-

Table 3. Adult emergence patterns for *Psorophora columbiae* reared in predator-exclusion cages in Louisiana rice fields.

| 1983 | | 1984 | |
Date	Emergence (%)*	Date	Emergence (%)*
Aug. 5	42.4a	July 5	35.7a
Aug. 12	45.2a	Aug. 3	45.1a
Aug. 18	40.4a	Aug. 5	42.4a
Aug. 26	43.2a	Aug. 17	52.3a
Harvest		Harvest	
Sept. 1	76.4b	Aug. 31	76.5b
Sept. 8	60.7b	Sept. 7	64.3b
Sept. 15	41.0a		
Sept. 22	44.4a		

* Means followed by the same letter are not significantly different ($P>0.05$).

pend on changes in larval survival rather than on variations in the number of eggs laid. If so, these data may justify the integration of strategies for the management of post-harvest larval populations.

Of the 26,000 *Ps. columbiae* larvae monitored over all dates, 53.3% successfully emerged as adults. There were no significant differences ($P>0.05$) in adult emergence detected between the cages monitored daily for survival and those monitored only at emergence. The sex ratios of emerging adults were constant during these investigations with no significant differences ($P>0.05$) detected among dates and resulted in an average male: female ratio of 1.11:0.89. There was a highly significant difference ($P<0.01$) between the laboratory and predator-exclusion survival rates although no significant differences existed ($P>0.05$) between sex ratios.

The factors responsible for the mortality and survival patterns documented in this study are unknown and hard to assess. Results from paired-*t* tests indicated that mortality within the predator-exclusion cages was not attributable to differences in any of the aquatic parameters measured. Laboratory investigations indicated that, at densities within observed field values, intraspecific competition had no effect on larval survival. Thus the data presented should be indicative of maximum field survival.

SURVIVAL OF NATURAL POPULATIONS. Table 4 indicates that the survival rates of a natural larval population decreased from 0.62 for the younger to 0.37 for the older age classes. The calculation of confidence intervals indicated that discrepancies due to sampling were a source of error in calculating these survival rates. More careful sampling will provide samples more representative of the population and therefore reduce biases and systematic errors but not the sampling error, which depends on the variability among individuals and

Table 4. Mean daily survival rates for natural populations of *Psorophora columbiae* larvae in Louisiana rice fields.

Day	Mean no. larvae collected (CI95)[a]	Survival rate[b, c]
0*	148.6 (45.2)	—
1	92.1 (23.7)	0.62a
2	55.3 (13.7)	0.60a
3	27.1 (6.8)	0.49a
4	10.6 (2.7)	0.39b
5	3.9 (1.0)	0.37b

* Sampled ca. 18 hr following post-harvest flood and represents the initial population density.

[a] Expressed as mean no. larvae/0.1m² (95% confidence interval).

[b] Expressed as probability of a larva surviving the next 24 hr.

[c] Means followed by the same letter are not significantly different (P > 0.05).

sample size. The sample size (450 dips/field/day) was as large as feasible and consequently, the survival rates given here may be regarded as approximations. Calculation of survival rates was discontinued at pupation (day 5) due to the inability to quantify adult emergence and the failure of the dipper to precisely estimate pupal densities (Andis et al. 1983).

The curve describing the survival rate of a natural population (Fig. 2) was more linear than in the absence of predators, with mortality having a more severe effect on the older larval age classes. These results are similar to those obtained by Service (1977) for *Anopheles* populations in rice fields that had been sprayed with phosphamidon. Initially, treatment with this systemic organophosphate had virtually eliminated the predator populations. However, when predators recolonized the field they were more effective on the older age classes.

The survival values from the laboratory, predator-exclusion, and natural population studies were converted into percent mortality (Table 5). Subtraction of the field mortality, induced by factors other than predation, from the laboratory mortality rates indicated that the daily mortality occurring in the absence of predators is relatively constant and thus of little importance to *Ps. columbiae* population dynamics (Morris 1957).

The mortality inflicted by all indigenous natural enemies was estimated by the difference between total mortality and non-predator induced mortality (Table 5). From these data, it can be inferred that predation may, in fact, be restricted primarily to the older age classes, and manifest itself by a reduction in larval survival and ultimately as a reduction in the adult *Ps. columbiae* population density. Predators con-

Table 5. Estimates of total daily mortality for larval *Psorophora columbiae* that were attributable to predators and that attributable to other factors.

Day	Mortality (%)		
	Non-predation	Predation	Total
1	6.0	24.0	30.0
2	10.0	26.0	36.0
3	14.0	37.0	51.0
4	11.0	50.0	61.0
5	7.0	56.0	63.0
6	4.0	—	—

sumed at least 24% of the larvae in each field, a maximum of ca 56%, and apparently were the most significant mortality factor for immature *Ps. columbiae* in the rice fields studied. There may be additional mortality factors, for instance, shortage of necessary substances (i.e. food), the presence of harmful substances at a concentration sufficiently high to influence survival and emergence (i.e. insecticides), parasitization, drying, etc., but, as suggested by the predator-free survival rates, they are minor in usual circumstances. This supports the view of others that the predator complex is a major source of irreplaceable mortality for immature riceland mosquitoes (Service 1977, Miura et al. 1978, Mogi et al. 1980a, 1980b, 1984) and yields considerable credence to the hypothesis that natural enemies should be an important component of the developing riceland mosquito management program.

The total mortality of *Ps. columbiae* larvae was large and only 2.6% of the larvae survived to the pupal stage in the presence of predators. If one gravid female produces 160 viable eggs, 4 adults emerge under the absence of egg and pupal mortality, which means that 1 of the 2 females (sex ratio is 1:1) must take blood and lay eggs successfully for the population to be kept at a constant level.

These data should aid in the establishment of a suitable relationship between larval and adult *Ps. columbiae* population indices and in the establishment of an acceptable riceland mosquito management program in Louisiana through the use of treatment threshold values for larval *Ps. columbiae* populations.

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