

A DYNAMIC LIFE TABLE MODEL OF *PSOROPHORA COLUMBIAE* IN THE SOUTHERN LOUISIANA RICE AGROECOSYSTEM WITH SUPPORTING HYDROLOGIC SUBMODEL. PART 1. ANALYSIS OF LITERATURE AND MODEL DEVELOPMENT¹

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ABSTRACT. During the past decade, the rice agroecosystem and its associated mosquitoes have been the subject of an extensive research effort directed toward the development and implementation of integrated pest management (IPM) strategies. The objective of this work was to synthesize the literature and unpublished data on the rice agroecosystem into a comprehensive simulation model of the key elements of the system known to influence the population dynamics of *Psorophora columbiae*. Subsequent companion papers will present a validation of these models, provide an in-depth analysis of the population dynamics of *Ps. columbiae*, and evaluate current and proposed IPM strategies for this mosquito. This paper describes the development of 2 models:

WaterMod: Because spatial and temporal distributions of surface water and soil moisture play a decisive role in the dynamics of *Ps. columbiae*, an essentially hydrological simulator was developed. Its purpose is to provide environmental inputs for a second model (PcSim) which simulates the population dynamics of *Ps. columbiae*. WaterMod utilizes data on weather, agricultural practices, and soil characteristics for a particular region to generate a data set containing daily estimates of soil moisture and depth of water table for 12 representative areas comprising the rice agroecosystem. This model could be used to provide hydrologic inputs for additional simulation models of other riceland mosquito species.

PcSim: This model simulates the population dynamics of *Ps. columbiae* by using the computer to maintain a daily accounting of the absolute number of mosquitoes within each daily age class for each life stage. The model creates estimates of the number of eggs, larvae, pupae, and adults for a representative 1-ha area of a rice agroecosystem.

INTRODUCTION

According to the Food and Agriculture Organization, rice is the staple food of half of the human race with the projected demand for this cereal expected to increase by almost 90% from 1975 levels by the year 2000 (Tsutsui 1984). Most rice-producing land in developing countries is flooded for relatively long periods of time and much of it subsequently produces disease vectors, including primarily snails and mosquitoes (Myers 1984). In the United States, rice acreage has increased ca. 55% during the past decade (N. G. Gratz, 1981, unpublished data, World Health Organization). This expansion was accompanied in many areas by a significant increase in the abundance of several species of riceland mosquitoes (Paine 1983).

Researchers of the Riceland Mosquito Management Project (RMMP) and the closely associated ARS/CSRS Regional Project on Riceland Mosquitoes (S-122) have been directing multi-institutional and multi-disciplinary research efforts toward the development and implementation of better integrated pest management (IPM) schemes against mosquitoes arising from the rice agroecosystem of the United States since 1977. These efforts are based on the premise that "mosquito populations associated with such systems are . . . among the most likely targets for the immediate application of IPM strategies since they have adapted themselves to habitats which are already largely under human control and have become rather dependent upon man and his land use practices for their continued existence" (Olson 1983).

A major objective of the RMMP and S-122 programs is to develop a better understanding of the rice agroecosystem as it pertains to mosquito production by means of systems analysis; this work represents a contribution toward that goal. This objective stems from the belief that improved control of riceland mosquitoes will come from a more rigorous understanding of the population dynamics of the mosquitoes coupled with the development of new and/or improved control and survey techniques. Systems analysis through computer simulation is a useful and necessary tool in the understanding of the com-

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plex interactions between environmental and biological factors of the rice agroecosystem. The development of models allows an integration of the current base of knowledge; it highlights areas where additional information is required and can be used to develop estimates of population parameters that are difficult to obtain from field studies. Additionally, because large-scale field trials are expensive, simulation is an important adjunct to the development, evaluation, and optimization of IPM schemes. Finally, the simulation model of *Psorophora columbiae* (Dyar and Knab) could be used in an expert system designed to aid mosquito abatement personnel with control decisions on a day-to-day basis.

Major rice growing regions of the United States include California and the southern states of Texas, Louisiana, Mississippi, and Arkansas. In southern rice areas, the dark rice field mosquito, *Ps. columbiae*, is the major periodic (or floodwater) mosquito pest of humans and animals. It was a primary vector of Venezuelan equine encephalitis (VEE) when this virus was introduced into the United States in 1971 (Sudia and Newhouse 1971, Sudia et al. 1971, Olson and Newton 1973). In addition, it is known to adversely affect livestock production (Steelman and Schilling 1977, Steelman et al. 1972, 1973). Because of its importance in southern rice areas, this floodwater species was selected as a primary target of the RMMP/S-122 investigators.

In the rice agroecosystem of the southern USA, *Ps. columbiae* breeds in temporary pools such as swale areas and grassy roadside ditches, soybean and rice fields, and pastures (Schwardt 1939, Horsfall 1942, 1955; Meek and Olson 1976, 1977; Curtis 1985, Welch et al. 1986). The winter months and dry periods are spent primarily in the egg stage. Oviposition occurs directly on the earth and at locations and elevations where soil moisture ranges between 75 and 100% of field capacity (FC) (Olson and Meek 1977, 1980). The number of generations of *Ps. columbiae* each season is limited primarily by the frequency of inundation of eggs with water of summer temperatures (Horsfall 1955). While many factors influence larval and pupal survival, a requisite to immature survival and subsequent adult emergence is the continued presence of surface water until near the time of eclosion (Al-Azawi and Chew 1959).

The major objective of the effort reported here was to develop a comprehensive simulation model of the key elements of the rice agroecosystem that influence the population dynamics of mosquitoes. Because the spatial and temporal distributions of surface water and soil moisture play such a decisive role in the dynamics of *Ps. columbiae*, an essentially hydrological simulator

(WaterMod) was developed to utilize data on weather, agricultural practices, and soil characteristics for a particular region to generate a data set containing daily estimates of soil moisture and depth of water table for representative areas comprising the rice agroecosystem. This model was also designed to provide hydrologic inputs for additional simulation models of other riceland mosquito species.

In the present work, WaterMod provides environmental inputs to a second model which simulates the population dynamics of *Ps. columbiae* (PcSim). The major attributes of PcSim include: 1) developmental times of immatures as a function of daily water temperatures derived from air temperatures, 2) survival of immatures as a function of larval density and habitat, elapsed time since a particular habitat was flooded, and the presence of surface water, 3) survival of adults as a function of soil moisture and host density, 4) the proportion of diapausing and non-diapausing eggs deposited in the fall as determined by day length and air temperature, 5) survival of eggs as a function of the diapause status of the egg and by the duration and severity of freezing temperatures during the winter, and 6) the habitat and elevation where oviposition occurs as a function of land use patterns, irrigation and drainage events, weather as it influences the spatial and temporal distribution of surface water and soil moisture, and the searching ability of females to locate appropriate oviposition sites.

This paper describes the development of these models from a synthesis of the literature and unpublished data. Subsequent companion papers will provide validation of the models presented here, present an in-depth analysis of the population dynamics of *Ps. columbiae*, and evaluate IPM strategies for this mosquito.

WaterMod

Several comprehensive models are able to predict surface and subsurface hydrology on the basis of soil characteristics, topography, weather, and agricultural practices (e.g., Knisel 1980, Skaggs 1980). These models were deemed unsuitable for our purposes because they were difficult to use by non-specialists and, more importantly, required prohibitive amounts of detailed, on-site data. However, a common feature of the soil profile of rice growing regions, the shallowness of the impermeable hardpan (Horsfall 1942), allowed us to develop a simplified but adequate model for this agroecosystem.

Complete data requirements (inputs) for WaterMod are: 1) soil porosity, 2) depth of hardpan, 3) average depth and area of small, irregular surface depressions which can hold water (hereafter referred to as ponding area and

depth), 4) daily rainfall and pan evaporation rates, and 5) for each of the 10 representative rice fields, the date for the initial flood (used in field preparation) and the cutting date for the first crop harvest (see the section entitled "Nominal irrigation practices" below for details). The proportion of annual rainfall that is lost from the area in the form of surface runoff was used to compare predicted and observed rates as an evaluation of the model during validation (Focks et al. 1988a).

The output of WaterMod is a data set containing, for each day of the year, estimates of the daily water table depths in 12 locations, 10 within RICE, and one each representing the NON-RICE and DITCH/SWALE areas. We have retained the use of inches in this paper because soil hydrology continues to use the English system of measurement and the inch is a convenient degree of resolution for use in the models.

Both WaterMod and PcSim simulate a representative 1-ha area of the rice agroecosystem. This area is divided into 3 sub-areas on the basis of unique factors determining water balance in each location. While the hydrological sub-area named RICE corresponds with the rice field habitat, the other 2 divisions, NON-RICE and DITCH/SWALE, do not correspond directly to any particular agricultural habitat. The divisions, schematically represented in Fig. 1, are as follows: 1) RICE—represents land currently used for rice production. This area is further subdivided into 10 rice fields to allow modeling

the asynchrony in flooding, harvesting, etc. Unless all of first crop acreage is reflooded for a second crop, the proportion of land in this hydrologic category will decline during the year as first and second crop rice acreage becomes fallow following harvest. The unique feature of the RICE sub-area is the influence of water management practices: levees, irrigation, and draining; 2) NON-RICE—refers to land used for soybeans, sorghum, etc., and pastures, fallow or non-second-cropped rice fields. NON-RICE also contains an area considered not suitable for use by *Ps. columbiae*; this area would include areas of paving, buildings, lakes, wooded regions, etc. This non-suitable area is assumed to constitute two-thirds (67%) of the land in the NON-RICE hydrologic area. The unique hydrologic characteristic setting NON-RICE apart is the phenomenon of runoff, a result of rainfall in excess of that required to saturate the soil and fill small surface irregularities; 3) DITCH/SWALE—an area which represents the swale areas of pastures, soybean fields, etc., and roadside ditches and irrigation canals. Here, rainfall can collect and, as a result of runoff from NON-RICE, depths can become greater than the amount of rainfall. As will be seen below, while the 3 areas have specific hydrologic differences, they also share certain hydrologic similarities.

A description of the water balance calculations used to estimate water table depths in the 12 representative locations are as follows:

Water gain. When the water table is below the surface in any area, the initial fate of additional

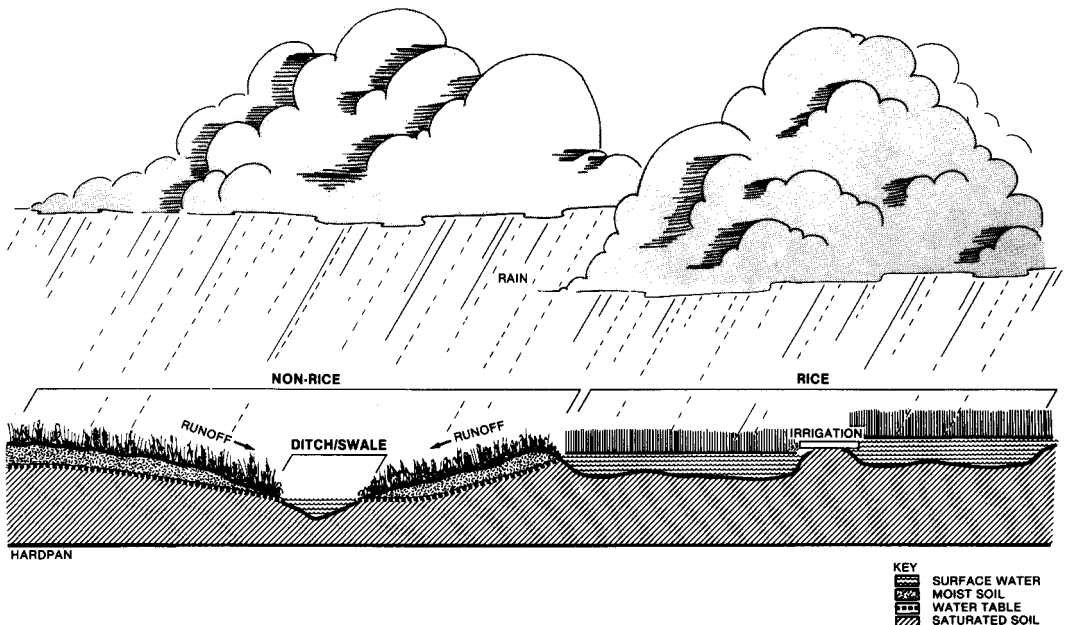


Fig. 1. Schematic representation of the hydrology of the rice agroecosystem with sources of water shown.

water, whether from rain, flooding, or runoff from another area, is assumed to infiltrate the zone between the water table and the surface by an amount determined by the soil porosity and the depth of the water table. In the present case, using a value of 0.01 for porosity in southwestern Louisiana (J. L. Fouss, personal communication), a 0.1" (0.25 cm) rain would be expected to raise the water table by 10" (25.4 cm). Water in excess of that required to bring the water table to the surface then accumulates in small irregular surface depressions (ponds). For cultivated lands in southern Louisiana, the average pond depth is ca. 0.7" (1.8 cm) and the combined area of such depressions is ca. 15% of the total area (J. L. Fouss, personal communication); for rice fields that were rutted by equipment during first crop harvest, values for pond depth and ponding area were estimated to be 4" (10.2 cm) and 15%, respectively (based on Meek and Olson 1977). The destiny of water in excess of that required to satisfy soil porosity and surface depression storage requirements varies by sub-area. Excess in NON-RICE accumulates as runoff in DITCH/SWALE; because NON-RICE serves as a watershed for the smaller DITCH/SWALE area, water depth in DITCH/SWALE is programmed to increase 3" (7.6 cm) for each inch of runoff. In RICE, when the levees are intact, excess water either from flooding or rainfall simply accumulates as surface water, i.e., a flooded rice field. When the levees are cut, RICE behaves like NON-RICE.

Normally, a simplified model such as WaterMod would be subject to a significant accumulation of error over the course of a few months if it were used to predict hydrology for areas with a deep impermeable layer and subject to significant lateral movement of sub-surface water. However, the proximity of the hardpan limits the significance of sub-surface water movement and results in even modest rains bringing the water table to a known point, i.e., the surface. This second ramification of a shallow hard pan allows the model to accurately revise its estimate of the depth of the water table every time there is a significant rain. For ex-

ample, given a soil porosity of 0.01 and a hardpan depth of 50" (127 cm), even under the driest antecedent moisture conditions, in areas where excess surface water is lost as runoff (see description of NON-RICE area below) all rains > ca. 0.5" (1.3 cm) bring the water table to the surface permitting any accumulated error in model estimation to be eliminated.

Water loss. Water losses common to all 3 sub-areas include surface evaporation and evapotranspiration. As a simplification, reduction in rates of loss from the water surface due to increasing plant canopy was assumed to be associated with corresponding increases in evapotranspiration losses. Daily loss from surface water and soil moisture was programmed to occur at 95 and 80%, respectively, of the pan evaporation rate (J. L. Fouss, personal communication). Water loss in NON-RICE occurs as runoff on the day an excess is received. In RICE, an additional water loss occurs when a field is drained or rain occurs when the levees are cut. Rice fields were programmed to drain a maximum of 3" (7.6 cm) per day (unpublished data). In addition to evaporation losses, the DITCH/SWALE losses were programmed to occur at a rate proportional to water depth (25% per day) to reflect greater flow in ditches with increased water depth. In RICE and DITCH/SWALE, when water depth equals pond depth, water balance is calculated as in NON-RICE. Because the hardpan is near the surface, WaterMod assumes no lateral subsurface movement of water.

Nominal rice irrigation practices. WaterMod generates individual water tables for 10 hypothetical first and second crop rice fields based upon antecedent rain and the dates of initial flood for field preparation in the spring and first crop cutting for each field. As some fields are planted sooner than others, this feature permits simulating the asynchrony of water events associated with rice production. With the exception of the wider latitude granted for water depths during the second crop, the scheduling of events was programmed to follow the practices of a grower in Jefferson Davis Parish, La. (D. Hollier, personal communication). Briefly the nominal schedule is as follows:

<u>Date</u>	<u>Day</u>	<u>Agricultural Event</u>	<u>WaterMod</u>
March 1	60	Flood for water leveling and seed bed preparation in fields which have been plowed earlier in the year. Water depth maintained at 3-4" (7.6-10.2 cm) for ca. 3 weeks.	Water depth increases 2" (5.1 cm) per day to 4" (10.2 cm). Thereafter, additional water added when depth declines below 2" (5.1 cm) from evaporation; depths >4" (10.2 cm) from rain are programmed to be lost as over flow.

<u>Date</u>	<u>Day</u>	<u>Agricultural Event</u>	<u>WaterMod</u>
March 25	84	Seeding by airplane.	
March 26	85	The field is now drained but maintained in a moist condition with rain or flushes if required to prevent the seed bed from cracking.	Drain programmed to reduce water depth a maximum of 3" (7.6 cm) per day until water exists only in surface ponds. Actual water table (WT) depth then varies as a function of rainfall, irrigation, and pan evaporation rate. If, from rain, water depth > pond depth, WT set to 0 (overflow). If WT < -30" (76 cm) from drying, WT set to 0 (flush).
May 1	121	First permanent flood put on; depth maintained between 2 and 3" (5.1 to 7.6 cm) by rainfall and/or additional irrigation water as required.	Water depth initially set to 3" (7.6 cm). Additional water added as evaporation reduces depth below 2" (5.1 cm). Depths >3" (7.6 cm) from rain are programmed to be lost as overflow the next day.
May 21	141	Depth of permanent flood increased to a nominal 6" (15.2 cm) and maintained at this level via additional flooding or overflow when depths are <4" (10.2 cm) or >6" (15.2 cm), respectively, as a function of rain and evaporation.	Water depth initially increased to 6" (15.2 cm). Evaporation losses trigger water depth increase to this depth at 4" (10.2 cm). Transient depths greater than spillway height (6" or 15.2 cm) due to rain are reduced to spillway height the following day.
July 5	186	Levees cut to drain field prior to harvest.	As indicated for March 26 but without addition of water.
July 18	200	Harvest.	Pond depth increased to 4" (10.2 cm) because of tire ruts.
July 20	202	Two days after harvest, field is reflooded and water is allowed to range between bottom of 4"-tire ruts (-10 cm) and 6" (15.2 cm) above pan for 92 days for second crop. Water depths not maintained as accurately as in first crop.	As per the permanent, full flood of first crop except subsequent flooding triggered only when WT is slightly below bottoms of tire ruts. Maximum depth is limited by spillway height of 6" (15.2 cm).
October 1	294	Levees cut to drain field prior to second crop harvest.	See comments for WaterMod for July 5.
October 21	315	Second crop harvest.	See comments for WaterMod for July 5.

PcSim

We simulated the population dynamics of *Ps. columbiae* by using the computer to maintain a

daily record of the estimated numbers of individuals within each of the age classes of each life stage for each of the 12 representative areas of the rice agroecosystem mentioned previously

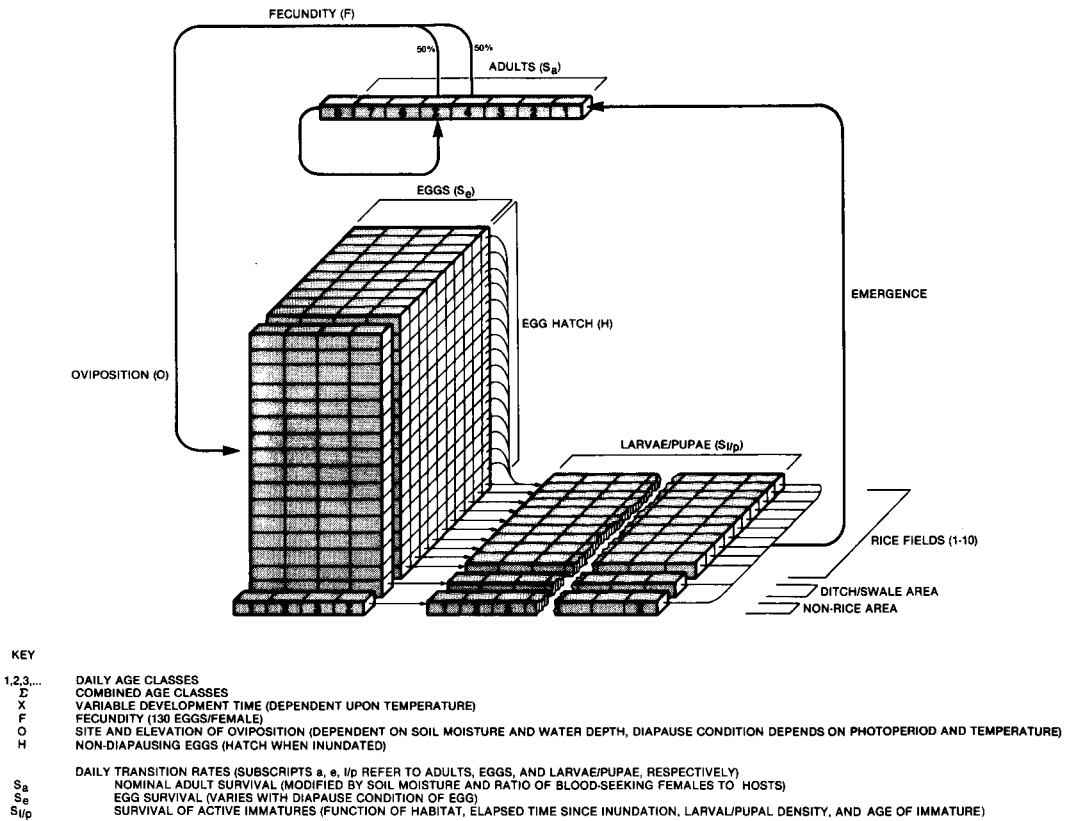


Fig. 2. Schematic representation of the life cycle of *Psorophora columbiae* in the rice agroecosystem. The boxes portray the various daily or combined age classes accounted for by PcSim. Computationally, they represent array locations within the computer which contain the absolute number of individuals per hectare. For the sake of clarity, a second egg array, identical to the one shown but containing diapausing eggs, is not depicted.

(10 rice fields of RICE, and the DITCH/SWALE and NON-RICE habitats; see Fig. 2). The accounting was made dynamic by recursively updating, in each area, each of the daily age class with the product of the number of individuals in the previous age class and transfer coefficients such as daily survival and fecundity, e.g., the number of 3-day-olds today is equal to the number of 2-day-olds yesterday times the proportion surviving from one day to the next. The development of active immatures was handled somewhat differently and is described below. Much of the balance of this paper will discuss how the transfer coefficients were determined and how they are modified slightly on a daily basis as a function of environmental conditions.

Termed appropriately a "dynamic life table" model by Haile and Mount (1987), this method has been used frequently in medical entomology simulation studies (e.g., De Moor and Steffens 1970, Haile and Weidhaas 1977, Focks et al. 1978, Mount and Haile 1987). Because of the rapid development of immatures at summertime

temperatures, the wide swings in survival due to daily fluctuations in environmental parameters, and the need to predict daily populations for abatement purposes, a resolution of one day was used in the model.

In addition to the daily hydrologic inputs from WaterMod, PcSim requires daily maximum and minimum air temperatures and, for each year of simulation, the proportion of land devoted to first and second crop rice. These proportions are used to determine the relative area of the NON-RICE hydrologic area; as discussed below, DITCH/SWALE area is fixed and does not change with changing RICE acreage.

FACTORS INFLUENCING IMMATURE SURVIVAL AND DEVELOPMENT

Temperature. Using daily data from the spring, summer, and fall of 1984 from U.S. Geological Survey (USGS) and National Oceanographic and Atmospheric Administration (NOAA) weather stations located within a rice field in Jennings, La. (D. Hollier, personal com-

munication), the following expression was developed for use in PcSim to predict a daily average rice water temperature (AvgWater) from the same day's maximum (MaxAir) and minimum air (MinAir) temperature ($^{\circ}\text{C}$):

$$\hat{\text{AvgWater}}_t = 9.65 + 0.30 * \text{MaxAir}_t + 0.48 * \text{MinAir}_t \quad R^2 = 0.80$$

For lack of data to enable us to do otherwise, this expression was also used to predict NON-RICE and DITCH/SWALE water temperatures. The proportion of total development that occurred each day was calculated using the enzyme kinetics model of Sharpe and DeMichele (1977) utilizing coefficients developed for *Ps. columbiae* by McHugh and Olson (1982). This model predicts the observed development not only along the linear region at mid-range temperatures, but also along the nonlinear region at elevated temperatures with a high degree of accuracy. The development time of larvae and pupae was made a function of temperature in the model by accumulating this daily proportion of development until emergence occurred at a sum ≥ 0.95 . With increments of ca. 10 to 20% of total development typically occurring on each day, programming emergence to occur at a value slightly less than one resulted in emergence occurring on the average at 1.0 because the accounting in PcSim is conducted on a daily basis.

Survival factors. Modeling the factors influencing immature survival was difficult due to a paucity of information in the literature dealing directly with *Ps. columbiae* immature survival. The methods and factors employed in the model represent a synthesis of the literature (Al-Azawi and Chew 1959, Andis and Meek 1985, McLaughlin and Vidrine 1986), discussions with Drs. J. K. Olson and M. D. Andis, literature reports on permanent-water mosquitoes breeding in rice fields and temporary pools (Service 1977, Miura et al. 1978, Mogi et al. 1980a, 1980b, 1984), and in some instances, the results of simulation itself.

a. Nominal, habitat specific. As virtually all literature presents immature survival estimates on a hatch-to-emergence basis, we began by assigning a maximum probability of overall immature survival (MaxOSi) from match to eclosion for each habitat. This value reflects habitat-specific biotic and abiotic factors and does not include the effects of predation, density dependent mortality, or death due to the disappearance of surface water prior to eclosion. As presented in the following paragraphs, MaxOSi is reduced by these factors to produce a net overall immature survival which is in turn converted, based upon the proportion of development occurring on each particular day, to a value which is used

in daily simulation calculations. These daily values are calculated for each of the 10 fields of RICE and for the NON-RICE and DITCH/SWALE areas individually to reflect local variations in the modifying factors listed above.

The value used for MaxOSi in first and second crop RICE is 0.60. This value was extrapolated from field data on the decline in dipper counts of *Ps. columbiae* between 2nd and 4th instars in second-cropped rice fields immediately after the initial reflooding (McLaughlin and Vidrine 1986); the calculation was made after correcting for age-related changes in dipper efficiency (Andis et al. 1983). These data were obtained at larval densities below that where density dependent mortality is thought to occur (Al-Azawi and Chew 1959, Andis and Meek 1985) and, most importantly, prior to colonization with predators (REM, unpublished data). This estimate of 0.60 for MaxOSi in RICE is in close agreement with another field estimate of overall immature survival under predator-free conditions: Using predator-exclusion cages in southwestern Louisiana rice fields, Andis and Meek (1985) observed overall immature survivals to range between 0.50 and 0.75; the higher value was associated with the period following reflooding of second crop rice. Values for MaxOSi for the other areas, NON-RICE, 0.12 and DITCH/SWALE, 0.16, were a result of discussions with M. D. Andis and J. K. Olson.

b. Predation. A number of workers have indicated 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). Andis and Meek (1985) estimated in the case of *Ps. columbiae* that predation was also the most significant mortality factor in southwestern Louisiana rice fields, accounting for ca. 80% of all losses. Unlike mosquitoes which are typically found in permanent water, temporary-pool-breeding mosquitoes are commonly in largest numbers immediately after inundation when the aquatic habitat has yet to be (fully) colonized by predators.

To reflect an accumulation of predators subsequent to flooding in RICE and the attendant reduction in survival, MaxOSi is linearly decremented over a 28-day period subsequent to inundation to a minimum value of 0.12 or 20% of the starting value of MaxOSi. We would expect larvae to experience this lower survival in older and previously flooded fields where additional irrigation water or rain had raised water levels to the point of inundating eggs previously laid above the former water line. The value of 0.12, representing expected survival one or more months after the permanent flood, is a somewhat higher value than an average of 2 tentative field estimates for *Ps. columbiae*: 1) 0.10 for

overall immature survival in late, first crop rice (M. D. Andis, personal communication) and 2) 0.03 for late, second crop rice (Andis and Meek 1985). The final, decremented value of 0.12 for overall survival in RICE is, however, in almost perfect agreement with other reported values ranging between 0.01 and 0.07 (average 0.035) for anopheline survival in permanently flooded rice fields (Service 1977, Mogi et al. 1984, C. H. Schaefer, personal communication) when correction is made for the unusually short development period of *Ps. columbiae*: an overall survival of 0.12 translates into a daily survival of 0.654 at a summer-time development rate of 5 days, viz., $0.12^{(1/5)}$. The corresponding daily estimate for an overall survival of 0.035 is 0.658 if a field estimate of immature development of 8 days is used (e.g., *Anopheles quadrimaculatus* Say, J. A. Seawright, personal communication).

In the other 2 hydrologic areas, MaxOSi is similarly reduced daily until a minimum value of ca. 20% of the initial value is reached. In all areas, each occasion that surface water disappears and inundation subsequently occurs, MaxOSi is reset to its initial value and the daily decline begins anew. As would be expected, the frequency of the inundation/drying cycle and hence, the frequency of recolonization and, therefore, reset in PcSim, is greater in NON-RICE than DITCH/SWALE and least in RICE. Because of differences in the duration of surface water, the most common value for overall survival in RICE is 0.12; in contrast, the most common values for the other 2 areas are much closer to their initial and upper values, MaxOSi.

c. *Density dependence.* Al-Azawi and Chew (1959) observed that the size of 4th instars of *Psorophora confinnis* (Lynch-Arribalzaga) (members of the *Psorophora confinnis* complex, as is *Ps. columbiae*) tended to vary inversely with larval density in irrigation lanes of date groves (an area corresponding to the DITCH/SWALE area in the present models). They concluded that this probably indicated the effect of competition at high larval densities. In this habitat, larval densities ranged between 600 and 12,600/m² based on dipper counts converted to absolute estimates after Andis et al. (1983). While larval densities as high as 2,500–4,000/m² have occasionally been observed in rice immediately after the reflooding of a harvested rice field (Chambers et al. 1979, Andis and Meek 1984, McLaughlin and Vidrine 1986), a compilation of all density estimates indicates that an average maximal value would be ca. 1,000/m². From laboratory studies, Andis and Meek (1985) concluded that, at densities observed in rice, intraspecific competition had no effect on larval survival. However, extremely high densities have been observed in Louisiana (unpublished data) and Texas (J. K. Olson, personal commu-

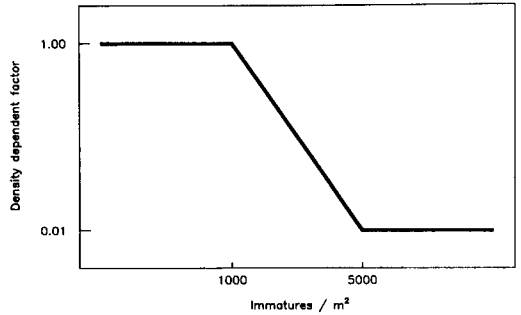


Fig. 3. The relationship between the density of active immatures and the density dependent factor, a term used in calculating daily immature survival.

nication) in ditches and swale areas as the habitat contracts from water loss. We therefore created a density dependent factor which ranges between 1.0 at low larval densities ($\leq 1,000/\text{m}^2$) to 0.01 at higher densities ($\geq 5,000/\text{m}^2$) (see Fig. 3). In the model, these values rarely result in any density dependent reduction in larval survival in rice fields. The factor does become operative in the DITCH/SWALE and NON-RICE areas where larval densities can occasionally become very high.

d. *Drying of temporary pools.* In addition to the factors mentioned previously, temperature, because it affects speed of development, and hydrologic factors, because they determine the duration of surface water, interact to determine the fate of a cohort of larvae. For example, Al-Azawi and Chew (1959) reported that *Ps. confinnis* were found only during the months of June through September in date groves in southern California. The principal temporary pools were irrigation lanes which were flooded on a bi-monthly basis. It was only during a portion of the year that temperatures were high enough to allow development before the habitat dried out about 5 days after flooding. Al-Azawi and Chew (1959) observed that 3rd instars stranded on moist soil invariably died, probably from starvation; when 4th instars and pupae were stranded, 44 and 91%, respectively, were able to complete their development.

Survival calculations. Because initial overall immature survival varies by habitat and larval densities and elapsed time since inundation are not necessarily the same for each site where larvae are present, daily survival values are calculated individually for each of the 12 locations. Computationally, they are equal to the product of the density dependent factor and the decremented value of the appropriate MaxOSi raised to the power of the proportion of development that occurred on that particular day as a function of temperature. If prior to emergence, surface water had disappeared resulting in the stranding of immatures on moist soil, the num-

bers emerging may be further reduced (depending on the degree of development that had occurred prior to stranding) by the amounts indicated in the preceding paragraph. Sex ratio of emerging males and females is set to 1.11 and 0.89, respectively (1.25) after Andis and Meek (1985).

FACTORS INFLUENCING ADULT SURVIVAL AND REPRODUCTION

Gonotrophic cycle and fecundity. Due to a lack of data, the length of the gonotrophic cycle of *Ps. columbiae* in PcSim is modelled as constant and independent of temperature (see Fig. 2). One-half of the females are assumed to oviposit during the 4th day of adult life and one-half during the next; subsequent oviposition cycles are 3 or 4 days in length. Blood meals are assumed to be taken on the day of emergence and on every other day thereafter; this results in 3 meals being taken prior to the first oviposition and one meal during each subsequent cycle. It is further assumed that all females are inseminated and lay a fixed number of eggs per gonotrophic cycle (130). The values used for gonotrophic cycle, blood feeding, and fecundity were derived from discussions with J. K. Nayar and from the literature (Horsfall 1955, Chapman and Woodard 1965, Nayar and Sauerman 1975a, 1975b, 1977); it is not possible to completely reconcile the observations of the previous workers with field observations by J. K. Olson (personal communication) that females spend the first 24–48 hr of adult life mating and migrating without blood feeding.

Nominal adult survival. In a fashion similar to that used in the calculation of larval survival, the determination of daily adult female survival begins with a nominal value (0.68) which is influenced by environmental parameters. The actual value for daily female survival used in calculations is the product of this nominal value and 2 environmental factors that reflect the influence of soil moisture and host density on survival. In simulation runs, during peak populations when host density influences adult survival (see below), daily survival values range between 0.59 and 0.63. These values are in fair agreement with unpublished estimates from 1) caged insects (J. K. Nayar, personal communication), 2) mean daily declines in sweep net captures around cattle (unpublished data), and 3) declines in the daily captures of 8 New Jersey light traps located in Acadia Parish, LA during 1984 and 1985 (unpublished data). Male survival is set to a constant 0.60 per day (J. K. Nayar, personal communication).

Influence of soil moisture on adult survival. The creation of a moisture factor was based on the observation (J. Billodeaux, M. D. Andis, J. K. Olson, and others, personal communication)

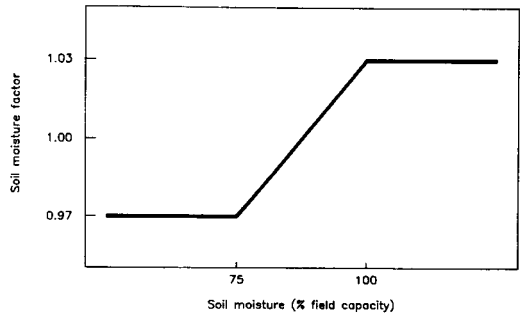


Fig. 4. The relationship between soil water conditions in the NON-RICE area and the adult survival soil moisture factor, a term used in calculating daily adult survival.

that a cohort of *Ps. columbiae* adults disappears more rapidly when humidity conditions are low. On this basis, we developed a factor related to soil moisture (Fig. 4) which ranged between 0.97 when the soil is dry ($FC \leq 75\%$) to 1.03 when surface water exists at a depth of ≥ 0 . The water condition in the NON-RICE area was used because it usually comprises the largest area within the rice agroecosystem. We considered using saturation deficit as a modifier of nominal survival as this would allow the roles of temperature and humidity to be integrated. However, because adults typically rest in low-lying vegetation (Schwardt 1939, Edman and Bidlingmayer 1969), preferring the underside of leaves or stems near the ground (Horsfall 1955), and select resting sites apparently in response to soil moisture during daytime when the deficit is usually greatest (Al-Azawi and Chew 1959), we reasoned that adult survival is probably more highly correlated with soil moisture than saturation deficit.

Influence of host density on adult survival. The purpose of including a second environmental variable was to make the model responsive to the influence of host density. As in the area of immature survival, there is very little information useful for the quantification of this relationship. We do know that cattle and to some degree, horses, serve as primary sources of blood meals in Texas ricelands (Kuntz et al. 1982) and that the availability of both blood and carbohydrate strongly influence fecundity and adult survival of *Ps. columbiae* on a nutritional basis (Horsfall 1955, Nayar and Sauerman 1975a, 1975b, 1977). It is clear that there is a relationship between variations in host density and mosquito abundance: Al-Azawi and Chew (1959) reported that adult densities averaged $0.8/m^2$ in irrigated groves without cattle as opposed to $9.8/m^2$ (a 13-fold increase) when (an undefined number of) cattle were present. Meek and Olson (1977) reported similar results: the average density of *Ps. columbiae* eggs was ca. 5 times greater

in fields with cattle than in fields where cattle were absent. A similar trend was reported by Chambers et al. (1981) and Williams et al. (1983). McLaughlin and Vidrine (1987), using regression, quantified the relationship between dipper counts in rice fields and cattle density within a 1-mile radius of the larval habitat; they observed a ca. 2-fold increase in larval density with an increase of 10 cattle/mi² (3.9/km²). We also know that host defensive behavior plays a role in limiting access to blood when *Ps. columbiae* populations are high (Horsfall 1942, 1955; Gahan et al. 1969). Finally, it would be understandable if lower host densities were to some degree associated with lowered rates of host finding.

The creation of a host density factor, the relationship between adult survival and the ratio of blood-seeking females to hosts (biters/host), necessarily represents a compromise and a simplification of what is known about the role of nutrition on fecundity and adult survival for *Ps. columbiae*. We have assumed, as did the mosquito models cited previously, that sugar availability in the environment is not a limiting factor. Furthermore, as we cannot partition the separate effects of host availability on fecundity and survival, we have chosen to attribute changes in reproductive success as a function of biters/host on the basis of its effect on adult survival alone, and not on its known role in influencing fecundity. We have assumed that a rise in the density of biters per host is accompanied by a decrease in female survival due to some combination of inadequate nutrition and mechanical factors, viz., missed or incomplete blood meals, death due to the increased defensive behavior of the host, and changes in the rate of host finding (Fig. 5). The values used in Fig. 5 were developed by simulation so as to produce the differences in population abundance similar to those seen in the field studies mentioned above. These values are within the range of *Ps. columbiae* attack rates observed on con-

finer cattle in Southern Louisiana (estimated from Steelman et al. 1972, 1973).

Oviposition site selection. There are records of *Ps. columbiae* adults being found 8 or more miles from their site of emergence (e.g. MacCreary and Stearns 1937). However, a review of all reports on the movement of this species indicates that typically, some 90% of all adults never fly more than a few miles from their larval habitat (Schwardt 1939, Horsfall 1942, Whitehead 1957). Examination of aerial photographs of the rice-growing region of southern Louisiana suggest that all habitat types are usually represented within any area circumscribed by the flight range of *Ps. columbiae* (R. E. McLaughlin, unpublished data). On this basis and because the consensus of many workers (Meek and Olson 1976, Williams et al. 1984, Rankin and Olson 1985, Welch et al. 1986, Welch and Olson 1987) is that, given adequate soil moisture, there are locations within virtually all habitat types found in the rice agroecosystem that are subject to *Ps. columbiae* oviposition, we have assumed the adult population to be mobile and capable, independent of their site of emergence, of ovipositing in any location as a function of water depth, soil moisture, ovipositional habitat preference, and land use. We believe a minor exception to the adequacy of the searching ability of *Ps. columbiae* females (discussed in paragraph c. below) occurs during dry periods in areas where rice acreage is very low and rice is the only habitat available for oviposition.

a. Distribution as a function of relative areas and soil moisture. A soil moisture $\geq 75\%$ FC, corresponding to a water table that is within 30" (76.2 cm) of the surface, is reported by Olson and Meek (1977) to be the range of adequate moisture. When all 3 hydrologic areas are sufficiently moist to attract oviposition, PcSim partitions the total oviposition available on that day as a function of each locations' relative area in the environment. There are some minor exceptions to this as noted in the following paragraph. Should RICE be the only moist area, all oviposition is placed in RICE. If NON-RICE is the only dry area, then oviposition is distributed among the RICE and DITCH/SWALE areas as a function of their 2 combined areas. The areas are calculated as follows: 1) The amount of land planted to rice changes from first crop to second crop and from year to year depending on a host of factors such as agricultural prices and government set aside policies; as a consequence, values for the proportion of land in first and second crop RICE for each year to be simulated are entered as data; 2) the DITCH/SWALE area is set to a constant of 10% of the total area (J. L. Fouss, personal communication); 3) the area of NON-RICE is the balance of the land. However, for the purposes of distributing oviposition, a

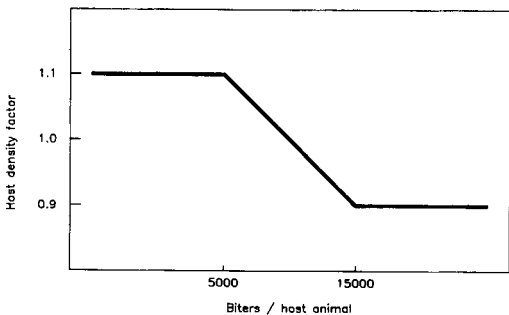


Fig. 5. The relationship between blood-seeking females per host and the host density factor, a term used in calculating daily adult survival.

portion of this area (called NOT-SUITABLE and assumed to be 67% of the NON-RICE area) is set aside as unsuitable for utilization by *Ps. columbiae* regardless of soil moisture. This is because NON-RICE includes, in addition to agricultural fields, areas of paving, buildings, lakes, lane without vertical relief, etc. If second crop rice acreage is less than first crop, the non-second-cropped acreage is moved from the RICE to the NON-RICE category as a rice field with cut levees behaves hydrologically like NON-RICE where, except for surface storage in tire ruts (corresponding to the irregular surface storage ponds of other NON-RICE areas), water is not assumed to accumulate.

b. Distribution modified by a preference for rice fields. An exception to a strict allocation as a function of relative areas which are moist stems from various accounts of a preference of *Ps. columbiae* to oviposit in harvested first crop rice fields. This preference is due to one or more of the following factors: 1) Increased relief is present as tire ruts from harvesting machinery (Meek and Olson 1977), 2) the "soil becomes firmer sooner, and the surface layer dries to dustiness much slower" and hence remains adequately moist for an extended period when compared to other areas (Horsfall 1955), also 3), the fermentation of soil and rice stubble may influence site selection (Gerhardt 1959). For these reasons, RICE was given a 30% preference for the month following harvest, a value determined through simulation by comparing the relative contribution of the various areas. Because WaterMod predicts soil moisture, the relative attractiveness of rice vs soybeans as a function of soil moisture reported by Welch and Olson (1987) required no special treatment. A second exception arises from the need to give NON-RICE and DITCH/SWALE slightly fewer eggs than would be expected on a strictly relative area basis because of qualitative reports that roadside and drainage ditches were not as important an oviposition site throughout the year as rice (Horsfall 1942, Meek and Olson 1977). For example, if 50% of all moist land suitable for oviposition was RICE, 50% of all eggs would be oviposited in RICE without an ovipositional preference; a 10% preference would result in 50 + 10 or 60% of the oviposition occurring in RICE. For simulation, throughout the year, RICE is given a 5% preference over the other 2 areas and this is increased temporarily after first crop harvest for 36 days to 30%.

c. Vertical distribution on levees and ditches. In addition to maintaining an accounting of the distribution of eggs by area (the 10 representative rice fields within RICE, NON-RICE, and DITCH/SWALE) and by diapause condition (see below), PcSim keeps track of egg locations

by vertical elevation in increments of one inch. The elevation of egg deposition varies by habitat and in response to soil moisture or the depth of surface water as the case may be at the time of oviposition. In NON-RICE, eggs are expected to be oviposited at the 0 elevation (i.e., within the small surface depressions) provided adequate surface water and/or soil moisture exists. DITCH/SWALE oviposition occurs equally at elevations 0 to 4" (10.2 cm) above the water surface or (providing adequate soil moisture) at the 0 elevation if there is no surface water (extrapolating from Olson and Meek 1980). In RICE, eggs are also uniformly laid between 0 and 4" (10.2 cm) above the water surface; without surface water but with moist soil, 95% of the eggs are laid in surface depressions (i.e., at the 0 elevation corresponding to oviposition on the surface of the pan) and 5% are placed uniformly on the bottom 4" (10.2 cm) of the levee (Olson and Meek 1980). If the soil is dry, oviposition still occurs in RICE but only at the bottom of the levee as this structure apparently retains water and remains moist at the base during otherwise dry conditions (Olson and Meek 1980).

d. Loss of oviposition due to dry soil conditions. As described to this point, if the soil in all areas becomes too dry for oviposition (or everywhere except RICE) and there are females ready to oviposit, all eggs are programmed to be laid in RICE. When rice acreage is not small, this probably reflects reality: the searching ability of *Ps. columbiae* females is sufficient to locate the only available oviposition sites under dry conditions, the rice fields. However under these circumstances, when rice is a small component of the system, we believe it reasonable to assume that an increasing proportion of females, after having left their site of emergence to obtain blood, either die prior to locating (relocating in the case of females emerging from RICE) the rice habitat or simply oviposit in inappropriate lo-

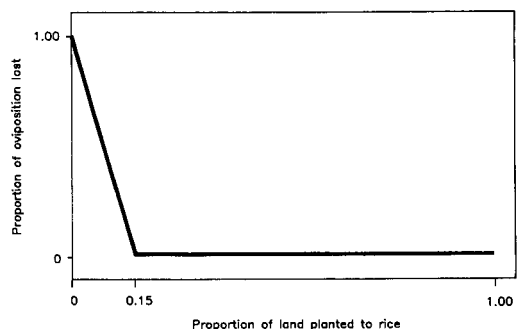


Fig. 6. The relationship between the loss of potential oviposition as a function of the proportion of land in RICE under dry soil conditions. See text for details.

cations. Figure 6 depicts the relationship used in PcSim to simulate this loss of potential oviposition as a function of the proportion of land in RICE: Whenever RICE acreage exceeds 15% of the total, all oviposition occurs as described previously. However, under the conditions of dry soil as indicated above, an increasing percentage of oviposition is lost when RICE acreage declines from 15% to zero.

Diapause condition, survival, and hatch of eggs.

As an overwintering mechanism, *Ps. columbiae* produces increasing proportions of diapausing eggs in the fall in response to temperature and photoperiod experienced by the larvae, pupae, and adults.⁴ PcSim inputs as data the proportion of eggs deposited in the diapause state; this proportion is determined manually using a model (Delorme et al. 1987) written for the Texas and Louisiana area which integrates the role of date and average air temperature to predict the proportion of eggs which are laid in the diapause condition each day. At the latitude of southern Louisiana, this proportion typically goes from 0 to 100% diapause during September.

Because rice and other crops are usually rotated each year, we assume that tillage destroys or buries 85% of all overwintering eggs in RICE and ca. 67% in NON-RICE. For the remainder of the eggs, survival rates were set to 0.9985 per day for diapause eggs (a value slightly lower than that estimated by D. K. Lee, Texas A and M University, personal communication) and 0.9970 per day for non-diapause eggs. Depending upon rainfall, it is possible for diapausing eggs that were deposited at the higher elevations not to be flooded and hatched until late spring or early summer. To reflect the exhaustion of energy reserves (after Olson and Meek 1979), etc., of older diapausing eggs, diapausing eggs are assumed to survive at the 0.9985 rate until mid-June, at which time their survival rate changes to that of non-diapausing eggs (0.9970/day).

Based on the premise that prolonged sub-freezing temperatures are lethal to eggs (J. K. Olson, personal communication), overwintering survival was reduced by a factor reflecting both the duration and the severity of freezing temperatures, e.g., the number of degree days below freezing (DDBF) (see Fig. 7). For example, a single day with an average air temperature of -3°C between warmer days would correspond to 3 DDBF. Looking at Fig. 7 indicates that this would not be expected to reduce egg survival. However, 3 consecutive days with temperatures

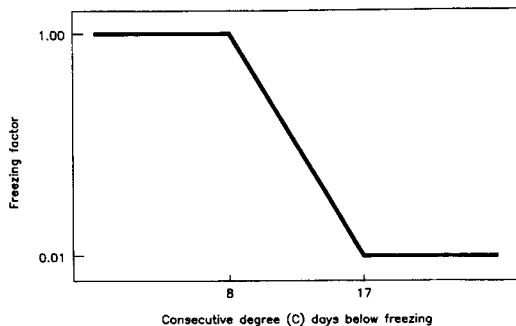


Fig. 7. The relationship between the product, degree ($^{\circ}\text{C}$) days below freezing (DDBF), and a freezing factor which is used in calculating a reduced overwintering egg survival. See text for details.

of -5 , -6 , and -2°C , corresponding to 13 DDBF would be significant as temperatures are low enough and for a period sufficient to freeze a proportion of the eggs in the environment. For each day or series of consecutive days with average temperatures remaining below freezing, the number of degree days below freezing is calculated and the corresponding freezing factor (as indicated in Fig. 7) is applied to the nominal overwintering survival values presented previously. The values used in Fig. 7 do not result in egg loss for most years in southwestern Louisiana. We recognize that this treatment is an oversimplification of the real situation, however, as elsewhere, data are not yet available to permit a more refined or sophisticated treatment.

Each day, all non-diapausing eggs 4 or more days old and therefore old enough to have completed embryonation (Horsfall 1942), are assumed to hatch when submerged (see Fig. 2). While we suspect that temperature and increasing day length would influence the date of breaking diapause, until we have data to allow a more sophisticated treatment, diapause is assumed to break on the first of April when both types of eggs are permitted to hatch (J. K. Olson, personal communication). A somewhat arbitrary date of October 31 is set as the last date for non-diapause egg hatch (unpublished data).

SUMMARY OF PROGRAM FLOW AND MODEL OUTPUT

WaterMod and PcSim were written and compiled with a version of BASIC⁵ that allowed the creation of highly modular and structured code on an IBM-AT⁶ personal computer. Our com-

⁴ Delorme, D. R. 1984. Egg diapause in *Psorophora columbiae* (Dyar and Knab): Development of a predictive diapause induction model. Unpubl. Diss. Texas A and M University. 95 p.

⁵ BetterBASIC (version 2.1) by Summit Software Technology, 106 Access Road, Norwood, MA 02062.

⁶ International Business Machines Corporation, P.O. Box 1328, Boca Raton, FL 33432.

puter was equipped with 3 M-bytes of random access memory (RAM), a 60 M-byte hard disk, and an Enhanced Graphics Adaptor (board) (EGA) and EGA monitor; the programs may be run on any IBM-compatible machine with a minimum of 512 K-bytes RAM and EGA graphics capability. Lotus 1-2-3⁷ was used for the creation of various input files and the display and plotting of output files. Program listings of both models may be obtained by contacting the senior author.

For each year to be simulated, WaterMod is first run to create a file which contains daily estimates of water table depths for the 12 areas used to represent the rice agroecosystem. This output data set from WaterMod is later read as input by PcSim where it is used to determine where oviposition occurs, where eggs hatch, where larvae are stranded, etc. At the start of each run of WaterMod, values for certain parameters which will remain constant throughout the year are input, e.g., soil porosity, hardpan depth, ponding area and depth, and the dates for initial flooding and first crop cutting for each of the 10 representative rice fields. To model the population dynamics around a single town or location, dates for 10 nearby rice fields are used; in this case, a particularly large field may be represented by 2 or more of the 10 hypothetical fields. Alternatively, to simulate the overall dynamics of a large area such as a parish, the dates for each of the 10 representative fields will correspond to observed dates when 10, 20, . . . , 90, and 100% of the acreage in the parish have been flooded initially or cut. After initialization with values for the parameters listed above, WaterMod then sequentially reads as input, a file containing observed values for rainfall and pan evaporation for each day of the year.

Similar to WaterMod, the output of PcSim is also a data file containing daily estimates, in this case, estimates for the entire year of the absolute density of all life stages of *Ps. columbiae* on a per m² basis for each of the 12 locations. Each simulation run begins with an initialization phase where data which remain constant throughout the simulation year are input. The first input file contains values for large animal host density and the relative proportions of land used for first and second crop RICE, DITCH/SWALE, NON-RICE, and land "non-suitable" for oviposition by *Ps. columbiae*. A second input data set contains estimates of the number of overwintering eggs from the previous year.

By initializing with the distribution of overwintering eggs found on the last day of the

previous year, a series of sequential years may be simulated. An initial egg distribution was developed by starting the model with a nominal egg distribution (100 eggs/m² in DITCH/SWALE and the "suitable" area of NON-RICE); the resulting eggs on the last day of this run were then used to initialize the next year, and this year's the next, etc. After 5 years, the distribution of overwintering eggs remained constant from year to year and reflected the influence of host density, weather, and land use. This distribution is used to start a series of simulation runs for the years of interest.

On a daily basis, PcSim reads as input a file containing maximum and minimum air temperatures, and the proportion of eggs deposited in the diapause condition and the hydrologic file produced by WaterMod. For each day, the model then proceeds as follows: For immatures, 1) larvae and pupae are aged as a function of temperature using an enzyme kinetics model, 2) the numbers of active immatures are adjusted in each area as a function of habitat, age and presence of surface water, and larval density, 3) hatch and emergence are programmed to occur where appropriate, and 4) eggs are aged according to their diapause condition and the time of the year. Next, 1) oviposition occurs as a function of current land use, soil moisture, and oviposition site preference and 2) adults are aged using a common survival value which is a function of moisture and host density.

For the purpose of understanding the actual population dynamics of *Ps. columbiae*, absolute densities of the various life stages as predicted by PcSim are examined. However, for the purpose of comparing expected adult densities from the model with light trap data from the field for model validation, the influence of several additional factors are considered: 1) The first is a physiological factor. The model assumes that newly emerged adults (e.g., <24 hr of age) do not come to light traps and therefore does not include 1-day-old mosquitoes when making density estimates which are to be compared with light trap data. 2) Low night time temperatures are assumed to reduce trapping efficiency by either moving the swarming period of *Ps. columbiae* adults forward in time and prior to nightfall or by simply reducing flight activity. To respond to this meteorological factor, model output is modified by a temperature factor (Fig. 8) which ranges between 1.0 at minimum night-time temperatures $\geq 15.5^{\circ}\text{C}$ to 0 at temperatures $\leq 5^{\circ}\text{C}$ (J. K. Olson, personal communication). This factor does not kill mosquitoes (i.e., the internal accounting of the actual number of adults on an area basis), it simply reduces the proportion of adults expected to be seen in light traps as a function of lower temperatures. 3) The final

⁷ Lotus Development Corporation, 161 First Street, Cambridge, MA 02142.

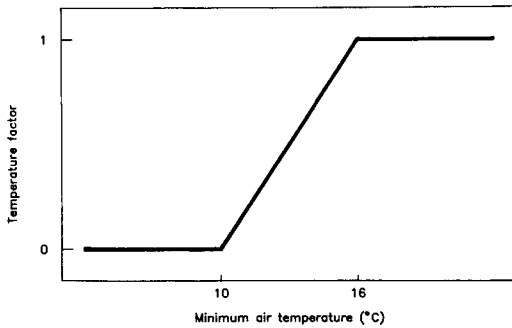


Fig. 8. The relationship between minimum air temperature and a temperature factor used to modify expected light trap captures on cooler nights. See text for details.

factor involves the scaling of light trap data. These data are reported simply as the number of adults captured. However, PcSim outputs expected adult densities on an area (per m^2) basis. For the purposes of comparing these disparate series, we have assumed that light trap captures are linearly correlated with adult density in the "vicinity" of the trap, i.e., we assume that light trap captures are a measure of density. To facilitate a visual comparison of trap data (ranging between a few and many thousands of adults per night) and predicted densities which rarely exceed $100/m^2$, a scaling factor is used. This factor is simply the ratio of average captures during the period of simulation to the average adult density as predicted by the model.

A validation of the models presented here and an in-depth analysis of the population dynamics of *Ps. columbiae* in the rice agroecosystem and an evaluation of current and proposed and/or hypothetical IPM strategies for this mosquito are presented in subsequent companion reports (Focks et al. 1988a, 1988b).

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