

A DYNAMIC LIFE TABLE MODEL OF *PSOROPHORA COLUMBIAE* IN THE SOUTHERN LOUISIANA RICE AGROECOSYSTEM WITH SUPPORTING HYDROLOGIC SUBMODEL. PART 2. MODEL VALIDATION AND POPULATION DYNAMICS¹

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ABSTRACT. In an earlier paper, the development of 2 simulation models designed to describe the interaction between key elements of the rice agroecosystem and the population dynamics of *Psorophora columbiae* were presented (Focks et al. 1988a). The objective of the work reported herein was to validate these models with field data. The first model (WaterMod) predicts soil hydrology conditions as a function of weather, agricultural practices, and soil characteristics for a variety of habitats found within the rice agroecosystem which are utilized by *Ps. columbiae*. Using a continuous series of hydrologic data collected in southwestern Louisiana during 1984 and 1985, WaterMod was demonstrated capable of adequately predicting runoff rates and the temporal timing of soil moisture and surface water. The second model (PcSim) simulates the population dynamics of *Ps. columbiae* based upon a host of variables including the output from WaterMod. This model was validated by comparisons made with density estimates from the literature on the temporal and spatial distribution of various life stages and by correspondence with light trap data gathered during the same time and location as the hydrologic data. PcSim was seen to respond appropriately to host animal densities and unusual meteorological events occurring during 1984 and 1985 in southern Louisiana.

A discussion is presented of the interaction between agricultural practices and certain key factors of the life history strategy of *Ps. columbiae* which permit the unusually successful exploitation of the rice agroecosystem by this species. A subsequent paper will use these models to evaluate current and proposed IPM strategies for this mosquito (Focks et al. 1988b).

INTRODUCTION

Focks et al. (1988a) described the development of 2 simulation models which were designed to delineate the interaction between key elements of the rice agroecosystem and the population dynamics of *Psorophora columbiae* (Dyar and Knab). The first model (WaterMod) predicts soil hydrology conditions as a function of weather, agricultural practices, and soil characteristics for a variety of habitats found within the rice agroecosystem which are utilized by this temporary pool-breeding mosquito. Using the output of WaterMod, the second model (PcSim) simulates the population dynamics of *Ps. columbiae*. The objective of the modeling effort was to summarize current knowledge, identify areas where additional research would be useful, and, with the view of evaluating current and potential control strategies (Focks et al. 1988b), allow an

analysis of the system which would shed light on the key factors influencing the population dynamics of *Ps. columbiae*.

The present paper contains 2 sections: The first deals with the validation of the WaterMod and PcSim models using an extensive data set developed in southwestern Louisiana, USA. The second section presents, with the aid of these models, an analysis of the population dynamics of *Ps. columbiae* in the rice agroecosystem. A third paper in this series (Focks et al. 1988b), also based on these models, evaluates and makes recommendations regarding current and proposed IPM strategies for this mosquito.

VALIDATION OF MODELS

The *Psorophora confinnis* complex, of which *Ps. columbiae* and *Psorophora confinnis* (Lynch-Arribalzaga) are members, has a distribution ranging from northern USA, through Central America and the West Indies, and into South America to Argentina (Carpenter and LaCasse 1974). While the taxonomy of the complex is currently being reexamined, in the USA, *Ps. columbiae* is thought to be present east of the Rocky Mountains and south of the northern tier of states. The closely related *Ps. confinnis* is believed to be confined to California and perhaps Arizona and New Mexico (J. B. Woolley, personal communication). In the USA, where light trap data are regularly collected, *Ps. colum-*

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biae is rarely a pest problem outside of the rice-growing region of the south central states of Mississippi, Arkansas, Louisiana, and Texas (Horsfall 1942, 1955; Schwardt 1939). As a result, it was in this region that Riceland Mosquito Management Program (RMMP/S-122) research enabling a modeling effort was conducted on the factors influencing the population dynamics of *Ps. columbiae*. Data on this species outside of the USA, virtually limited to collection records, were inadequate for model-building or validation work.

Because a resolution of one day was used in both models, the validation of WaterMod and PcSim required rather extensive data simultaneously gathered on a daily basis on soil moisture and surface water in various habitats, weather, agricultural practices, and various estimates of mosquito abundance (Focks et al. 1988a).

While estimates of virtually all of the parameters used in PcSim came from research directed by RMMP/S-122 researchers, data for validation came largely from a specific research project⁴ conducted during 1984 and 1985. In this study, regular observations were made of a number of agricultural and natural factors thought to influence the population dynamics of major pest mosquitoes of the southwestern Louisiana rice producing parishes of Jefferson Davis and Acadia. This study was unique in that data on agricultural practices, soil moisture and surface water and associated dates, land use, weather, and large animal and *Ps. columbiae* larval and adult abundance were simultaneously obtained on a parish-wide basis. These data from Acadia, where there was no organized mosquito control, were used in the validation of both models. A brief description of the data sets follows:

Mosquito and host densities. Adult *Ps. columbiae* populations were monitored twice weekly with New Jersey standard light traps; a geometric mean of 24-hr captures from 4 traps (after Williams 1939) was used to provide a parish-wide average for comparison with model output. Densities of II- to IV-stage larvae (on a per-m² basis) were estimated from dipper counts in newly flooded second crop rice using the equations of Andis et al. (1983). Horse and cattle densities were measured within 0.5, 1.0, and 1.5 mi. (0.8, 1.6, 2.4 km) radii of adult traps and larval dipping sites.

Agricultural practices and land use. Water conditions in ricefields, soybean and sorghum fields, and in swales and roadside ditches were

observed weekly along a fixed, ca. 50-mile (80-km) route through representative areas of both parishes. Based on land use maps, aerial photographs, and data from the trek through the parish, the proportion of riceland being flooded, fully flooded, drained, harvested, second cropped, remaining fallow, etc. and associated dates were obtained. From these data, a data set of the dates of flooding, cutting, etc., for 10 representative fields for each year was created. These dates were integrated by WaterMod along with pan evaporation and rainfall data to create hypothetical but hopefully representative water table depths for use in PcSim.

Soil moisture. On the weekly survey through the parishes and on an almost daily basis at various specific sites within the parishes, the presence of soil sufficiently moist to receive oviposition in agricultural fields (corresponding to the NON-RICE hydrologic area of WaterMod) was recorded. Moisture conditions were determined using Horsfall's (1955) observation that gravid *Ps. columbiae* females will generally deposit their eggs on soil between the time that the earth is in a firm moist state and when the surface layer of the soil begins to appear dusty. These subjective measures correspond, respectively, to field capacities (FC) of slightly greater than 100% to ca. 75% (Olson and Meek 1977). Due to the upward flux of water above the water table, a soil moisture of ca. 75% FC at the surface results when the water table is within 30–36" of the surface (Focks et al. 1988a).

Weather data. Pan evaporation and maximum and minimum air temperatures were obtained from a NOAA station located ca. 19 miles to the west of the study site. The average of the rainfall at 4 light traps located in Acadia Parish was used to create a single, parish-wide series for input into WaterMod.

Land use and host density. Values for parameters used in PcSim to simulate the population dynamics of *Ps. columbiae* in Acadia Parish, Louisiana and not reported here or in Focks et al. 1988a are as follows: Percentage of land used for first and second crop rice in 1984 was 45.0 and 15.0%, respectively, and 38.3 and 15.3%, respectively for 1985. Parish-wide average large animal density for both years was 0.06 animals per ha (15.5/mi.²).

WaterMod

As described in Focks et al. (1988a), both WaterMod and PcSim model a representative 1-ha portion of the rice agroecosystem. Depending on input data sets, this may be used to represent an area as small as a few rice fields or

⁴ Study directed by R. E. McLaughlin while Research Entomologist at the Gulf Coast Mosquito Research Laboratory, ARS, USDA, Lake Charles, LA.

an area as large as a parish. The representative area is divided into 3 subareas on the basis of unique factors determining water balance in each location. Briefly, the divisions (schematically represented in Fig. 1 in Focks et al. 1988a) are as follows: 1) RICE—represents land used for rice production. This area is further subdivided into 10 hypothetical rice fields so as to permit simulating the asynchrony in flooding, harvesting, etc. with field 1 representing the first 10% of the rice acreage planted, field 2 the second 10%, and so on. 2) NON-RICE—refers to land used for soybeans, sorghum, etc., pastures, non-cultivated areas, and fallow rice fields. A proportion of this hydrologic area is considered not suitable for use by *Ps. columbiae*. 3) DITCH/SWALE—an area which represents the swale areas of pastures, soybean fields, etc., and roadside ditches and irrigation canals. For these 12 locations, WaterMod creates a data set containing estimates of daily water table depths: 10 within RICE, 1 for NON-RICE, and 1 for DITCH/SWALE.

In the following paragraphs, attention is drawn to what are probably commonly observed and appreciated facets of the hydrology of the rice agroecosystem. However, because soil hydrology is a critical element in the population dynamics of *Ps. columbiae* mosquitoes, these events, as predicted by WaterMod are presented here. The intention of this discussion is twofold: First, recalling the role of soil moisture and the depth and persistence of surface water on larval survival and site selection for oviposition (Focks et al. 1988a), the discussion provides a basis for understanding the interaction of hydrology, land use, and the biology of the mosquito (Figs. 1 and 2). The second objective of this section is validation . . . to demonstrate the facility of the model to realistically simulate those elements of soil hydrology in this environment (Fig. 3) which are critical to the dynamics of *Ps. columbiae*.

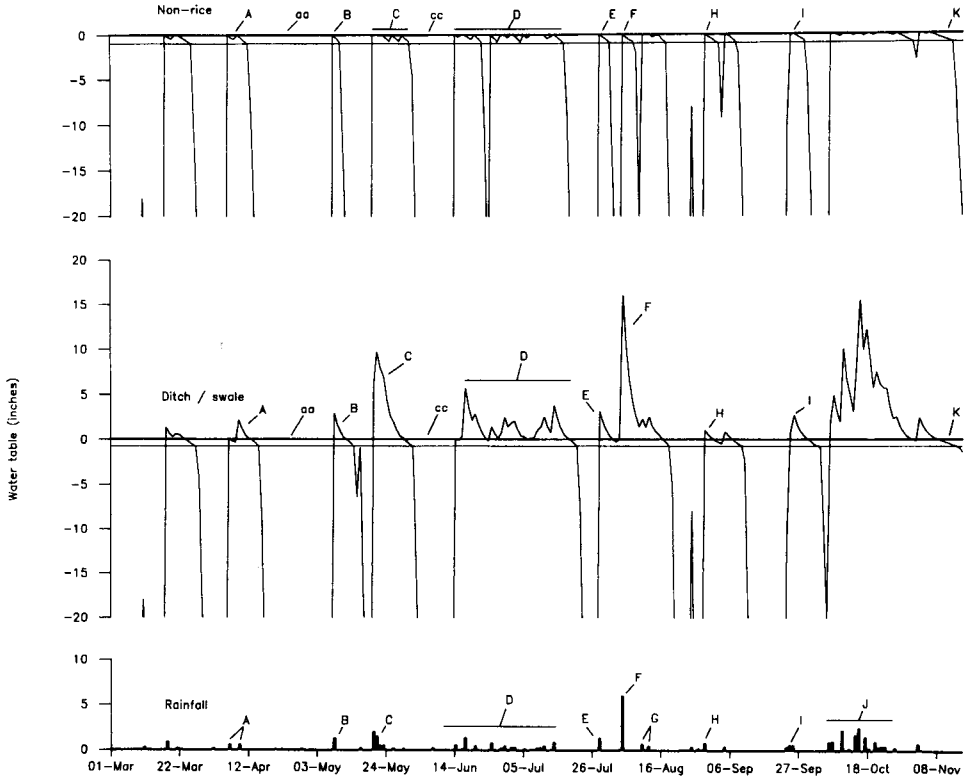
Based on soil and weather data from Acadia and Jefferson Davis parishes, Fig. 1 graphically presents water table depths in the DITCH/SWALE and NON-RICE areas as predicted by WaterMod for 1984 and 1985. For the sake of clarity, we have displayed water table depths ranging from 20" to -20" (ca. ± 50 cm) and for only that portion of the year when adults are active (March to mid-November). Major precipitation events in 1984 included a ca. 6" (15.2 cm) rain falling within a 24-hr period on August 4 and a series of thunderstorms late in the year which dropped unusually large amounts of rain throughout both parishes (labels F and J, respectively, Fig. 1a). Notable weather events in 1985 included hurricanes: Danny, Elena, and Juan (L, M, and N, respectively, Fig. 1b).

We can see from Fig. 1 that even small rains, for a short time at least, result in water in the small surface storage ponds of the NON-RICE and DITCH/SWALE areas (see A labels in Fig. 1a). However, because in NON-RICE, water in excess of that held in surface ponds is lost to runoff, larger rains in this area (i.e., in excess of that required to saturate the soil and satisfy surface storage requirements) do not increase the length of time that surface water persists (compare rains at B and F with the resulting persistence of corresponding surface water in NON-RICE, Fig. 1a). In this hydrologic area, the frequency of rains, more or less independent of their size, determines the duration of surface water (e.g., the series of rains denoted by D in the Rain and NON-RICE panels of Fig. 1a).

The situation is different in DITCH/SWALE. This area receives runoff from other areas and can retain water in depths greater than pond depth. Therefore, for any rain sufficient to produce runoff (a function of the amount of rainfall and antecedent moisture), DITCH/SWALE will have surface water in depths greater than the amount of rain and greater than in NON-RICE where maximum depths are limited to pond depth. A clear example of this occurred in response to 2 small rains in early 1984 (A, Fig. 1a): The first rain was adequate to saturate formerly dry soil and fill the irregular surface ponds in all areas; the rain was not so large as to produce any runoff however (i.e., resulting water tables were the same in NON-RICE and DITCH/SWALE). With the soil still saturated, the second rain was then more than enough to refill the surface ponds in both areas which had lost water to evaporation. The extra water in the larger area of NON-RICE was lost as runoff to the smaller DITCH/SWALE area. In DITCH/SWALE, the extra rain and subsequent runoff were retained resulting in greater water depths. As a consequence, throughout the year, surface water (and hence soil moisture) frequently persists longer in DITCH/SWALE than in NON-RICE.

A final comment regarding Fig. 1 concerns the rates of change in water table depth. The rapidity with which the water table changes in any area once surface water disappears is due to low soil porosity; it simply does not take a large water gain or loss to saturate or dry tightly packed clay. In DITCH/SWALE, losses are due to evapotranspiration and (when depths are greater than pond depth) surface flow into the low lying bayous. Because surface flow (at least in ditches) is proportional to depth, surface water declines most rapidly when depths are greatest (e.g., compare the slopes of the declines in water table depths in the DITCH/SWALE area at the times indicated by labels F and I,

1984 a



1985 b

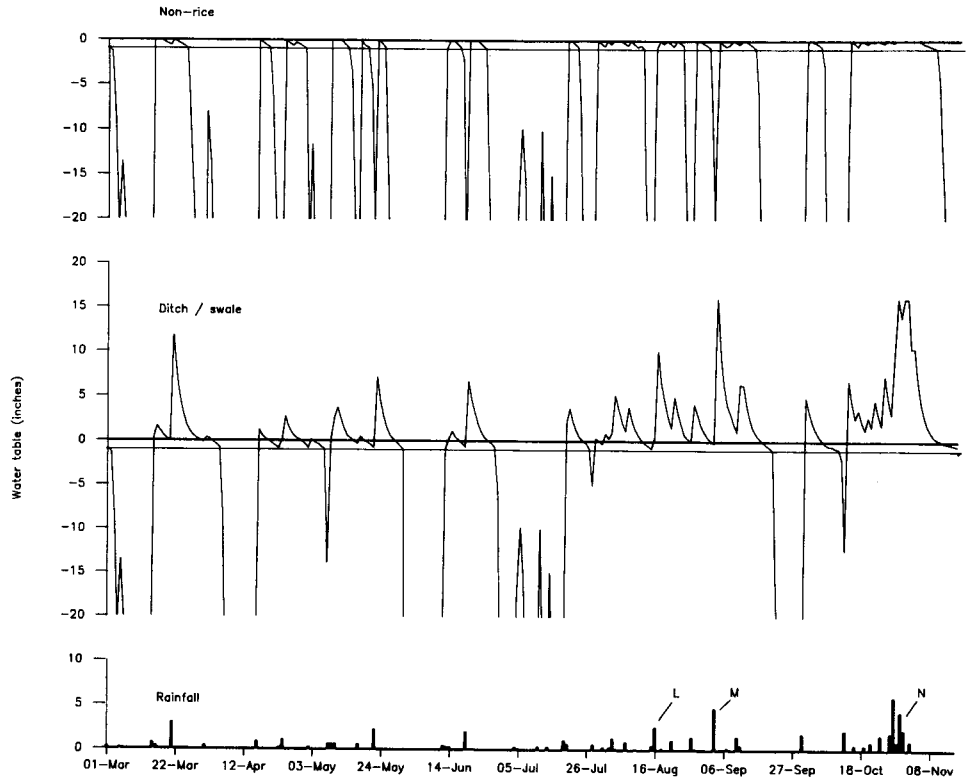
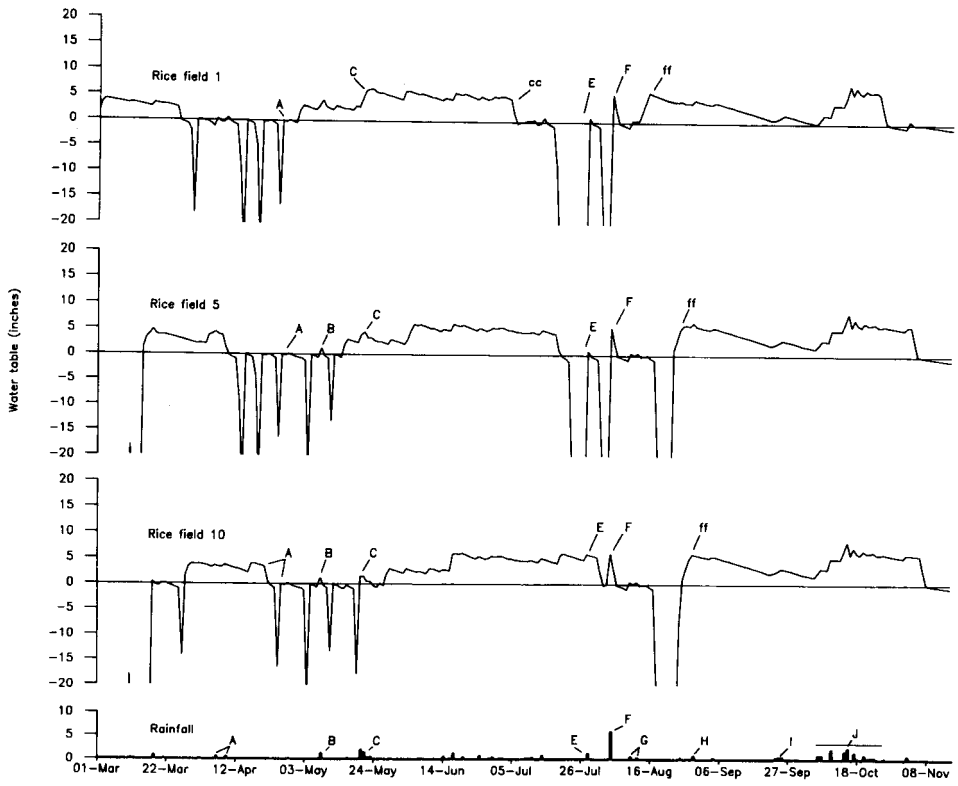


Fig. 1a and b. Water table depths in DITCH/SWALE and NON-RICE areas as predicted by WaterMod for 1984 and 1985 in Acadia Parish, Louisiana. Heavy, horizontal line at 0" elevation in upper panels represents ground surface; thinner line below represents the average elevation of the bottoms of surface irregularities (i.e., pond depth of surface storage ponds). Timing and amount of average rainfall at light traps indicated by vertical bars in bottom panel. Here and elsewhere, letters identify events discussed in the text.

1984 a



1985 b

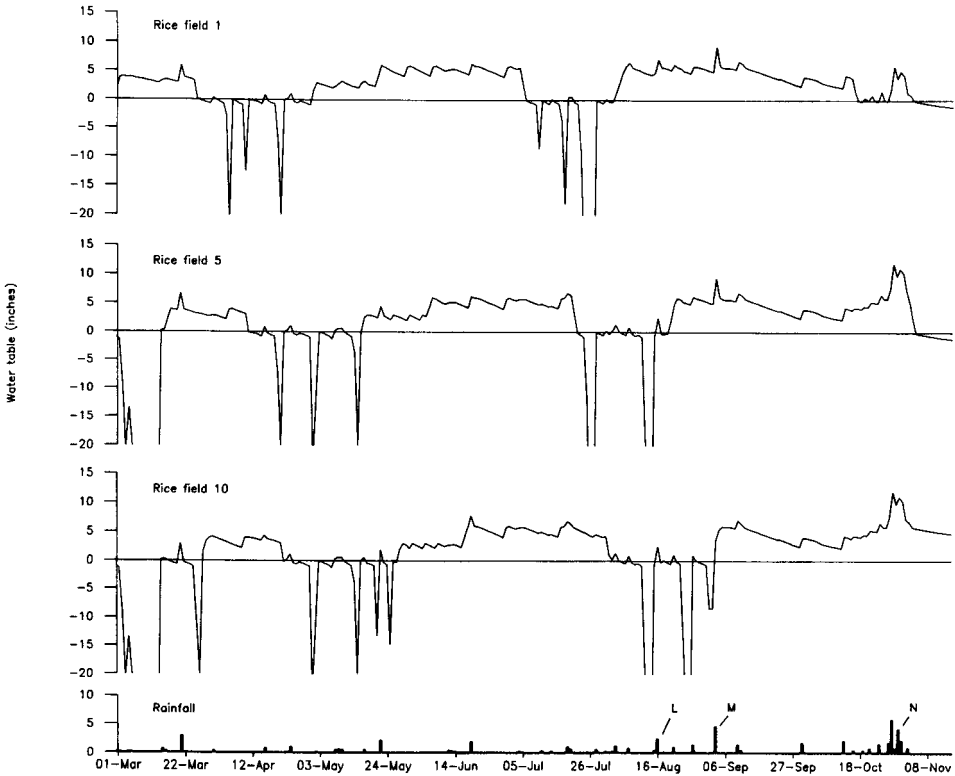


Fig. 2a and b. Water table depths in the 1st, 5th, and 10th hypothetical RICE fields as predicted by WaterMod for 1984 and 1985 in Acadia Parish. Rainfall indicated by vertical bars. Increased water depths not associated with rainfall on the same day are due to irrigation.

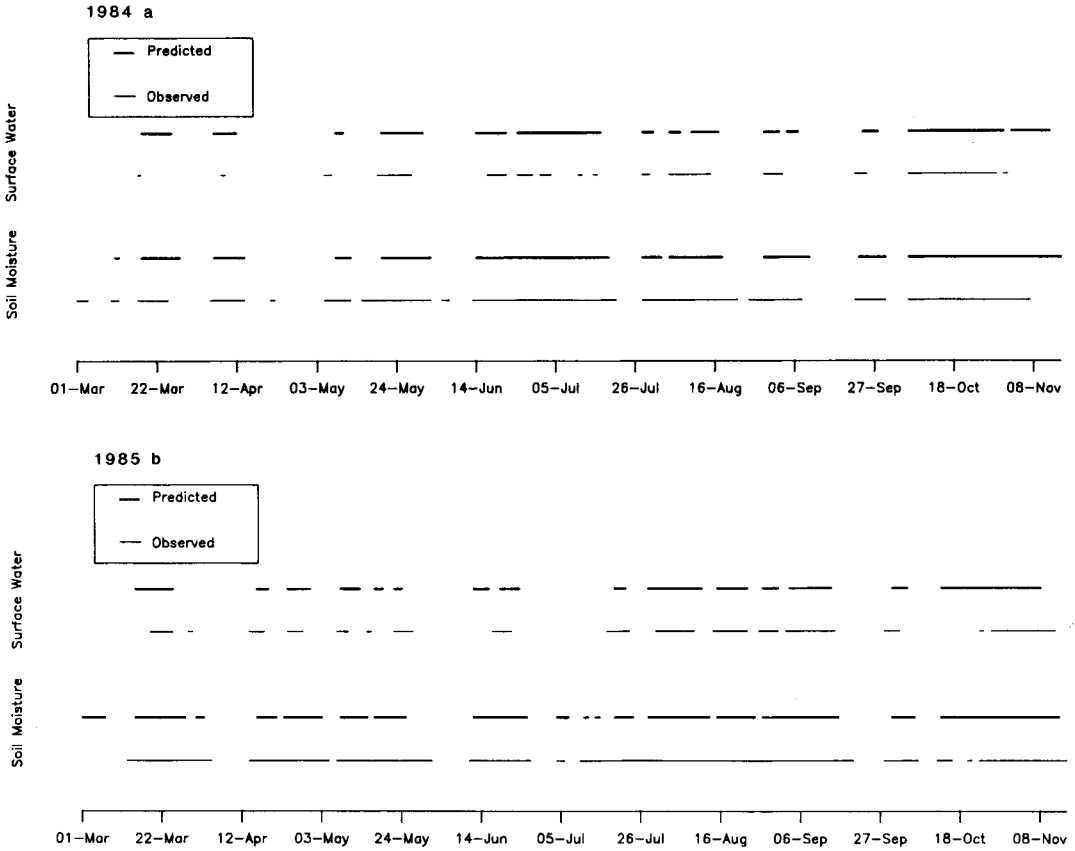


Fig. 3a and b. Observed and predicted times during the 1984 and 1985 *Psorophora columbiae* season when surface water was present and/or soil moisture was $\geq 75\%$ of field capacity in NON-RICE area of Acadia Parish.

Fig. 1a). The rate of water loss once water exists only in the irregular surface ponds is the same in either area and is determined by daily evapotranspiration as predicted by pan evaporation rates. The predicted rate of water loss in surface storage areas of either area was greater during early May than in mid-November (B and K, respectively, Fig. 1a) and was due to lower evaporation rates in the fall of the year. Although, as indicated above, the frequency of rain is paramount, the lower rate of loss in the cooler parts of the year would also be reflected in a somewhat greater persistence of moist soil during this time of the year.

Figure 2 is similar to Fig. 1 with the exception that projected water depths are displayed for some of the hypothetical fields of the RICE area for 1984 and 1985. For clarity, only 3 of the 10 fields are shown and they correspond to the 1st, 5th, and 10th fields to be planted. The timing of events in the 1st field corresponds to the nominal schedule presented by Focks et al. (1988a). The other 9 fields were created using the same nominal schedule as field 1 except, on the basis

of field data, they were started 0 to 4 weeks after field 1 to simulate the observed asynchrony of agricultural practices.

It can be seen in Fig. 2a that on March 1, Field 1 was flooded for a ca. 25-day period for leveling and seed bed preparation. Late in March, the field was seeded by air and then drained on the next day; for the following 35 days the field was prevented from drying to the point of cracking . . . in this instance, requiring 5 flushes (as compared with 3 in 1985) because of a lack of rain in the spring of 1984. The permanent flood (initially to a nominal depth of 3" or 8 cm) was applied shortly after label A. The subsequent fluctuations in water levels served until the levees were cut (at cc) prior to harvest resulted from evaporation, irrigation, and rainfall; the sharp depth increase at C represents the start of the full-depth (6" or 15 cm) flood. The peak at F reflects the rain of 6" (15.2 cm) which fell into the drained and drying field. This rain delayed harvest and subsequent re-flooding (label ff) for second crop (see below). Other differences between fields are the result

of the interaction between the irrigation/drainage schedule and the arrival of rain at different times in that schedule.

Figure 3 compares observed and predicted dates when surface water was present (top pair of broken lines) and when soil moisture (bottom pair) was approximate $\geq 75\%$ FC (i.e., water table $> -30''$ (76.2 cm)) in NON-RICE areas of Acadia Parish, Louisiana during 1984 and 1985. While we would not expect perfect correspondence, as there is error in both the observed data set and WaterMod, these figures do demonstrate that the model is capable of predicting soil moisture conditions with adequate accuracy based on reference to a rather limited set of standard hydrologic variables. The model tends to slightly overestimate the length of some periods when surface water was present and underestimate the length of periods when moisture $\geq 75\%$ FC; similar discrepancies were observed for 1985. A second measure of the adequacy of WaterMod was a comparison of predicted and observed annual runoff rates; the model predicted rates of 72 and 74% for 1984 and 1985, values which are in excellent agreement with a measured average runoff rate of 70% for non-rice agricultural areas of southwestern Louisiana (J. L. Fous, personal communication). Based on the good correspondence between the observed and predicted runoff, surface water, and soil moisture conditions, we feel that WaterMod is an adequate hydrological simulator for its intended use. The ability to predict the timing and relative abundance of natural populations of *Ps. columbiae* with PcSim based on the output of WaterMod supports this conclusion.

PcSim

The purpose of this section is to compare simulation predictions of the timing and density of adult and immature populations in response to weather and land use with observed densities of *Ps. columbiae* in Acadia Parish, Louisiana in 1984 and 1985. A more in-depth account of the interaction of the many factors influencing the dynamics of this mosquito follows in the next section on population dynamics.

Comparison of observed and predicted trends in adult populations. To allow a comparison of trap data (ranging from a few to many thousand adults per night) and predicted densities which rarely exceed $100/m^2$, a common scaling factor for both years was used in Fig. 4. This factor, applied to the light trap data, is simply the ratio of the average adult density as predicted by the model and the average captures during the period of simulation (0.0005). Because low nighttime temperatures influence trapping efficiency, the predicted captures in this figure are modified

as indicated by Focks et al. (1988a); comparing this figure with Fig. 9 (a plot of absolute densities) reveals that the only occasions during 1984 or 1985 when adults were present at times when temperatures were sufficiently low to influence captures was during October 2-6, 1984 (label I, Figs. 4a and 9a).

Figure 4 indicates that PcSim, in response to inputs from WaterMod, is capable of predicting fairly accurately the timing of major outbreaks of *Ps. columbiae*. The figure also indicates that predictions of relative abundance throughout the season and between years agrees with trends displayed by light traps in the area. An exception to this general correspondence between observed and predicted, the frequent over estimation of adults during late, first-crop rice, will be discussed below. In 1985, light trap operations ceased prior to the projected adult populations of October and early November of 1985 (J in Fig. 4b and 9b), however, high numbers were observed in the neighboring parish during this time (J. Billodeaux, Director, Jefferson Davis Mosquito Abatement District, Jennings, LA, personal communication). As will be elaborated below, the models followed observed population trends despite some unusual weather patterns in both years.

Comparison of observed and predicted egg and larval densities. Figure 5 presents predicted diapause and non-diapause egg densities per m^2 in the various hydrologic areas in 1984 and 1985. Evaluation of the correspondence between the real world and expected egg densities on anything approaching a day-to-day basis is hampered by a lack of data. Egg densities vary markedly over time with rainfall, irrigation, season, etc. (Welch et al. 1986). On the other hand, determinations of egg density are difficult and expensive to obtain. As a consequence, no continuous series of observations (analogous to light trap data) have been reported over time and (as eggs, unlike adults are immobile) for any of the various habitats. In addition, many estimates reported in the literature are undoubtedly overestimates as sampling sites are commonly selected on the basis of cues suggesting the presence of eggs with results being reported as averages of positive samples only; these data were frequently gathered to assess the utilization of or relative abundance within a particular habitat and not to develop an absolute estimate on a per-area basis. As a final complication, in almost all cases, egg estimates are reported without reference to nearby host densities. However, the following comparisons and generalizations can be made: The maximum diapausing egg density predicted to occur late in the season in RICE is in line with observed overwintering densities on pans and levees by Olson and Meek (1980)—

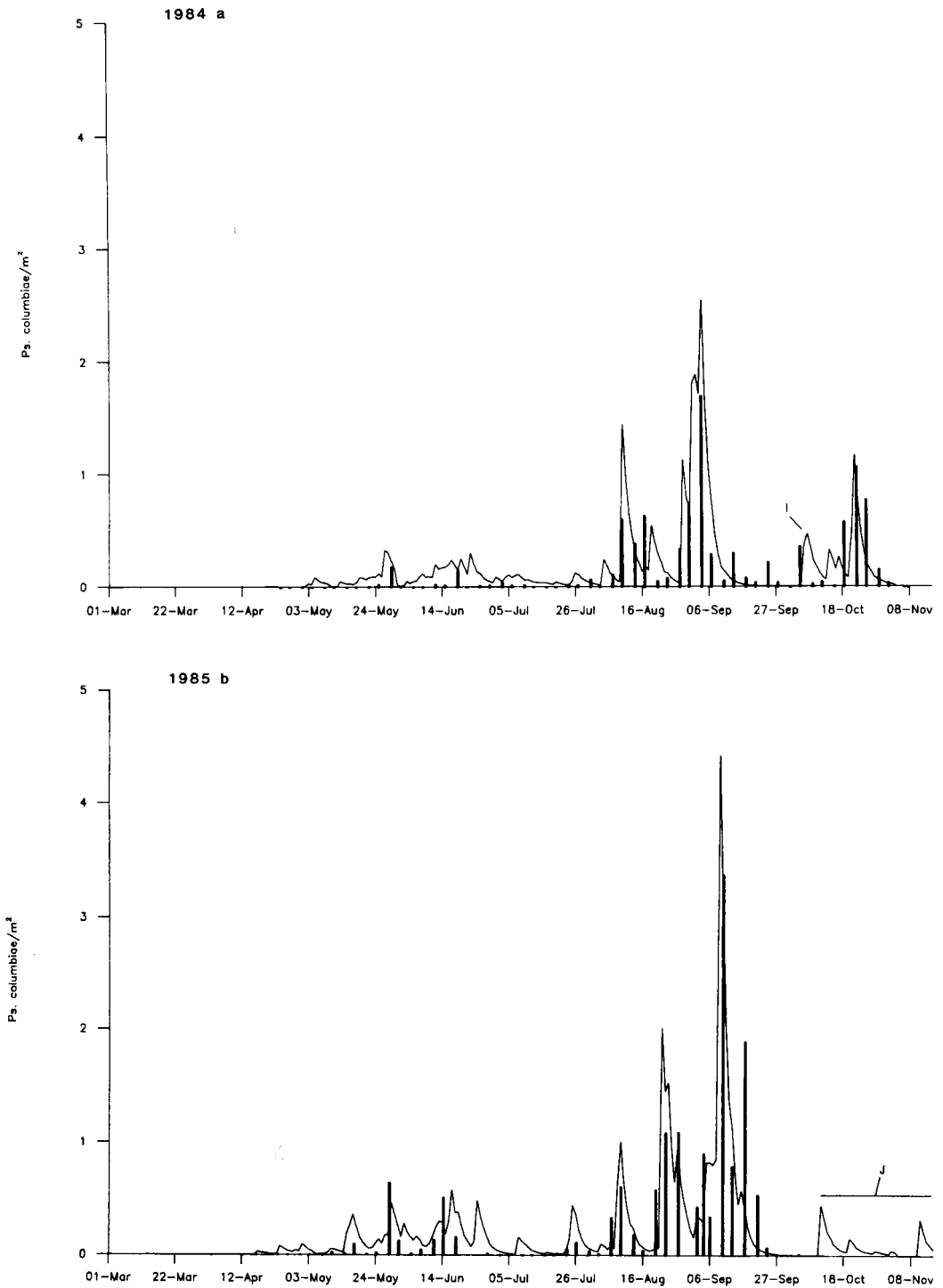


Fig. 4a and b. Comparison of the geometric mean of the catch of *Psorophora columbiae* in 4 New Jersey standard light traps operated 24 hrs. every 3 or 4 days (bars) versus expected adult densities per m² (1 or more days old) during 1984 and 1985 in Acadia Parish (lines). Light trap values scaled in both years by a factor of 0.0005 for comparison.

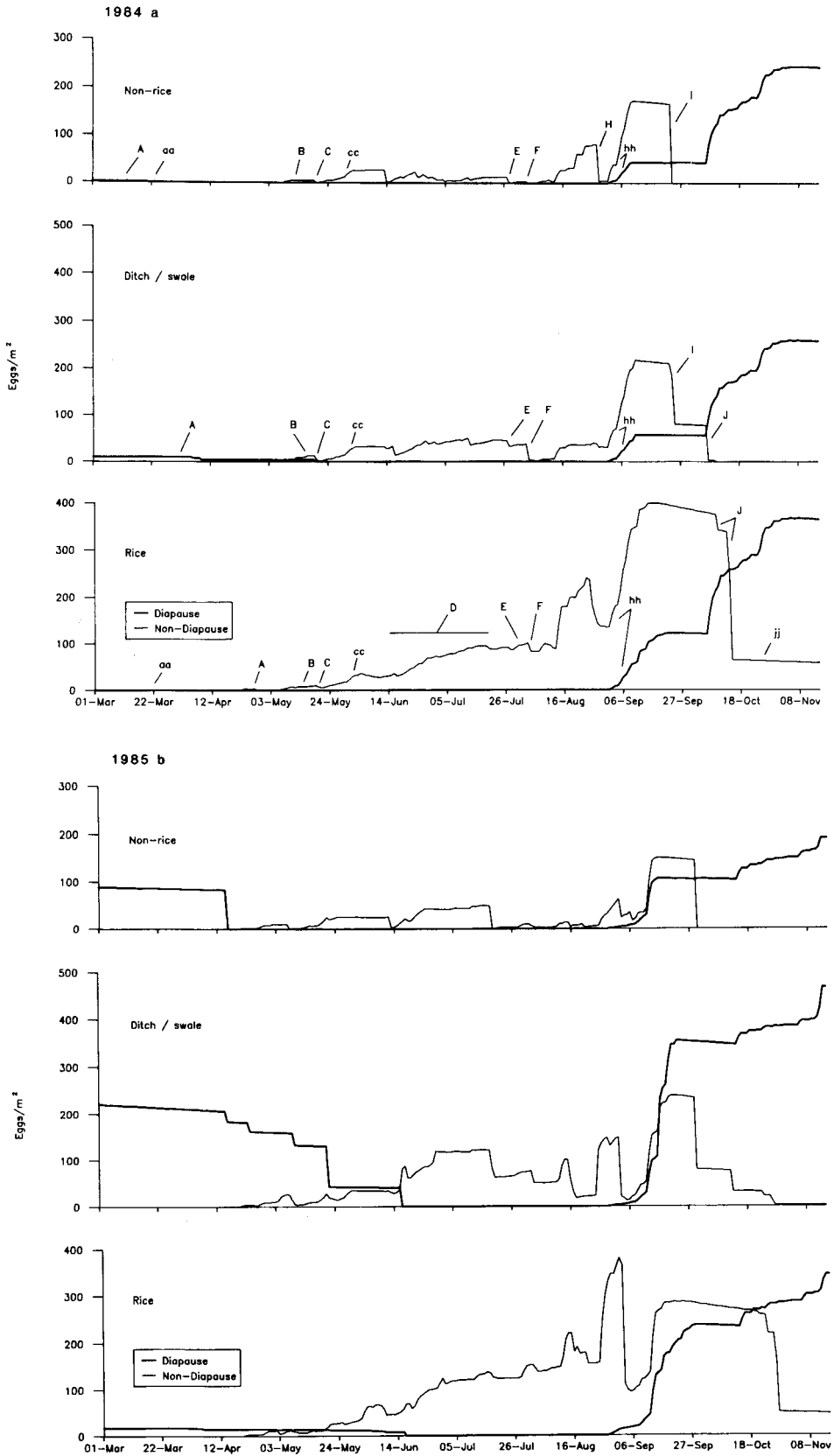


Fig. 5a and b. Plots of expected *Psorophora columbiae* egg densities per m² by hydrologic area in 1984 and 1985 in Acadia parish.

range: 200–235/m². The predicted densities in various hydrologic areas at various times throughout the year are also within ranges of values reported in the literature for *Ps. columbiae*, e.g., Meek and Olson (1977)—rice levees, range: 30–800/m²; Williams et al. (1983, 1984)—estimates within permanent pastures and fallow rice, areas corresponding to NON-RICE, range: 9–56/m²; Rankin and Olson (1985)—non-rice crops watered with sprinkler irrigation, average: 522/m² in soybeans, 263/m² in rice, and 106/m² in sorghum; Welch et al. (1986)—estimates throughout the year for various non-rice agricultural areas, range: 0–630/m² in soybeans, 0–150/m² in permanent pasture, and 0–260/m² in fallow rice. An average of the preceding estimates is 217 eggs/m². In summary, given the paucity of data and the volatility of egg abundance over time, we can conclude, as a minimum, that predicted absolute densities of eggs and their variability over time in various habitats are in line with observation.

Figure 6 presents predicted larval densities in the rice agroecosystem during 1984 and 1985. Again, without a continuous series of data, a day-by-day comparison between observed and predicted densities is not possible. Because larval densities have seldom been reported as a function of nearby host densities, the following generalizations can be made: The plots indicate that PcSim predicts average larval densities in RICE that fall within the range reported for *Ps. columbiae* in southern Louisiana by Chambers et al. (1979)—range: 0–1,727/m², Andis et al. (1983)—range: 0 to generally <1,000/m², McLaughlin and Vidrine (1986, 1987)—range: 0–3,234/m², and Craven and Steelman (1968)—range: 494–1,482/m². Andis and Meek (1985) concluded that intraspecific competition was not an important factor limiting larval survival or adult emergence of *Ps. columbiae* populations in southwestern Louisiana. In agreement with this, the larval densities predicted by PcSim for the rice habitat were at levels low enough to not be significantly influenced by density dependent mortality (compare Fig. 3 in Focks et al. 1988a with Fig. 6). And finally, while there are no NON-RICE larval densities reported in the literature, predicted densities in DITCH/SWALE are in agreement with anecdotal estimates of densities in Louisiana (REM, unpublished data) and Texas (J. K. Olson, personal communication).

Response of model to changes in host density. A previous study in southwest Louisiana (McLaughlin and Vidrine 1987) demonstrated a relationship between the density of large animals (primarily cattle) and larval densities (dipper counts) in nearby rice fields. Specifically, the study indicated: 1) the density of the first

cohort of *Ps. columbiae* following reflooding for second crop increased linearly with increasing host density within a 1.0 mi. (1.6 km) radius of the rice field being sampled, and 2) that reference to host density within this radius could explain ca. 60% of the variability in observed larval densities.

Figure 7 indicates that PcSim predicts larval densities that are almost identical with observed densities reported by McLaughlin and Vidrine (1987) for southwest Louisiana. Estimates from PcSim are an average of larval densities in the 10 representative fields of RICE 2 to 4 days after reflooding and converted to dipper counts after Andis et al. (1983). The model's projections are slightly curvilinear as a result of density dependent factors coming increasingly into play at higher population levels. This correspondence provides very firm evidence that the projected larval densities of the model are very likely accurate and would imply further that absolute adult and egg densities as a function of increases in host density in Fig. 7 are virtually identical suggesting that feedback mechanisms used to produce density dependence in the model are functionally correct.

A similar, unpublished study (R. E. McLaughlin) indicates an even stronger relationship exists between adult densities of *Ps. columbiae* and large animal abundance. Briefly, regression analysis indicated that no significant relationship existed between annual, average light trap captures and host density within a radius of 1.0 or 1.5 mi. (1.6 or 2.4 km) of the trap. However, host density within a 0.5 mi. (0.8 km) radius explained ca. 95% of the variability. Figure 8 presents a regression of these data scaled (as in the case of Fig. 4) so as to allow comparison with average, expected adult densities per m² from PcSim when run at a range of host densities found at various locations in Acadia and Jefferson Davis parishes. As in the case of larval density as a function of host abundance, the similar slopes of the observed and projected lines in Fig. 7 further suggest that the model responds appropriately to changes in host density.

The ratio of the averages of expected adult density per m² and observed light trap captures per night (also 0.0005 as in the case of Fig. 4), the scaling factor, represents a conversion factor between observed 24-hr light trap captures and expected adult densities on a per m² basis in nearby areas. For example, on the basis of the scaling factors derived here and for Fig. 4, a trap capture of 10,000 adults on a single night would correspond to an absolute *Ps. columbiae* density of 5 per m². While such a conversion does not reflect important factors such as the movement of adults, non-uniform distribution of adults and

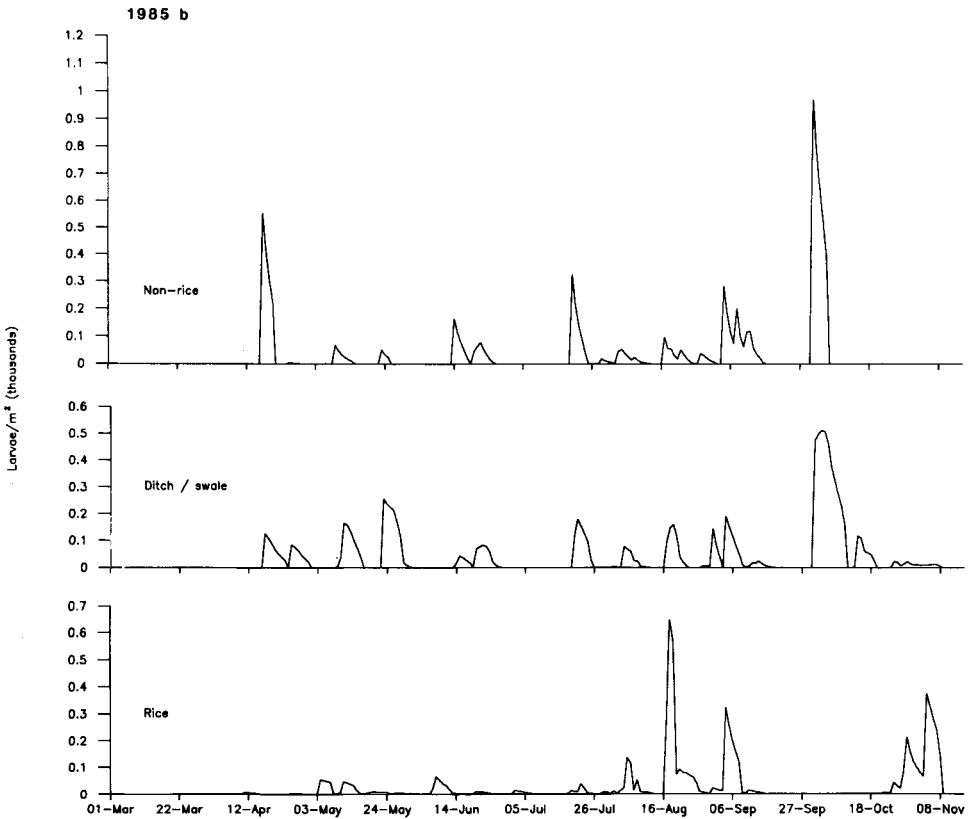
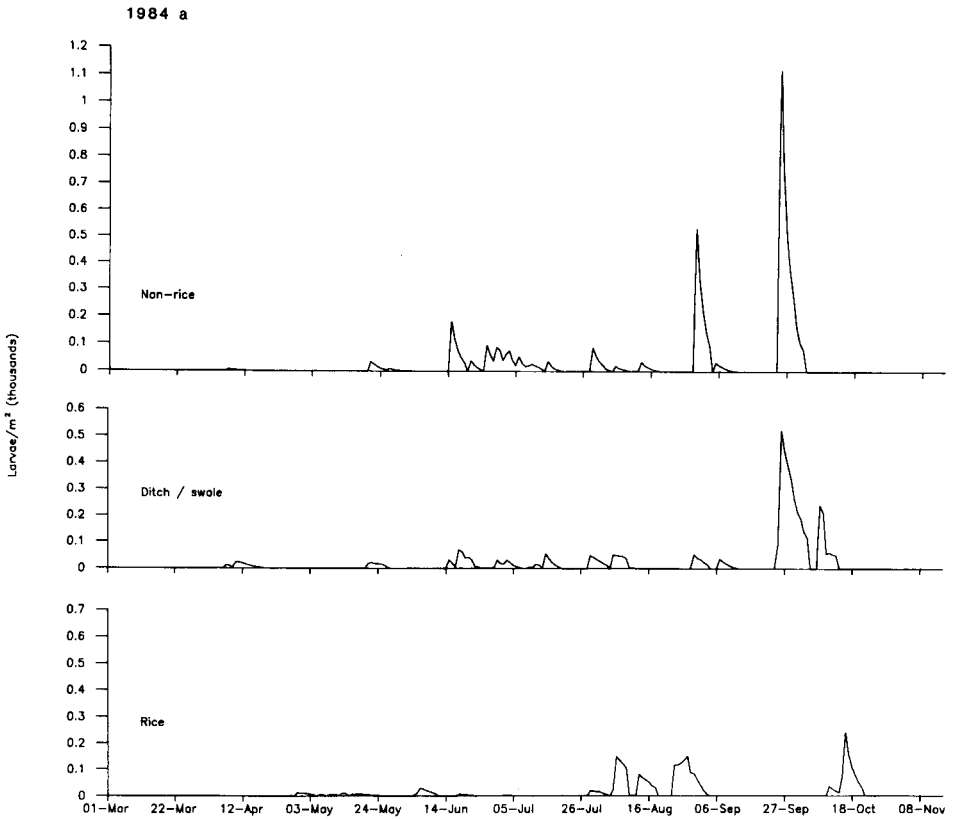


Fig. 6a and b. Plots of expected larval densities per m² in 1984 and 1985 in Acadia Parish by hydrologic area (hypothetical field 5 shown as representing the RICE area).

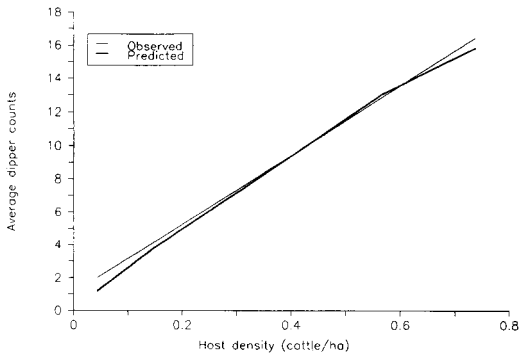


Fig. 7. Comparison of observed (McLaughlin and Vidrine 1986) and predicted dipper counts in second crop rice 2 to 4 days after reflooding versus cattle density within 1 mi. (1.6 km) of the larval sampling site. Predicted dipper counts calculated from PcSim's absolute density (numbers per m²) estimates using the equations of Andis et al. (1983).

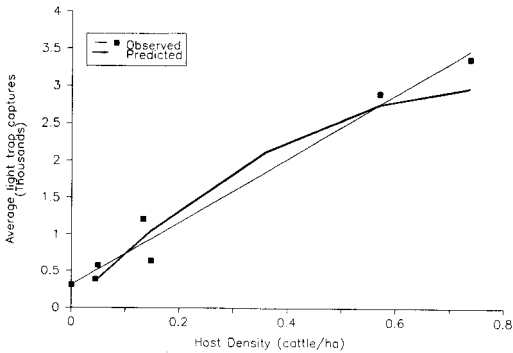


Fig. 8. Comparison of average observed (unpubl. data) and predicted adult densities versus large animal host density within 1 mi. (1.6 km) of the light trap. Observed adult densities are the season-long averages for 8 New Jersey light traps located in Acadia and Jefferson Davis Parishes. Predicted densities are from PcSim run at a range of host densities observed in the same area.

immatures, and influence of weather on light trap efficiency, it does provide the first reported method of relating light trap captures to associated absolute densities for this species. As will be seen in Focks et al. (1988b), the ability to know absolute densities is critical in the evaluation of control methods where the mode of action operates in a density-dependent fashion.

In summary, we believe that PcSim accurately simulates the population dynamics of *Ps. columbiae* in the rice agroecosystem of southwestern Louisiana. In addition, the ability to track the volatile changes in adult populations with PcSim provides further support of the adequacy of WaterMod. Light trap captures are noto-

riously difficult to predict. Yet, projected populations of adults agreed well, both with regard to timing and relative abundance, with average observed densities. As will be discussed below, this correspondence was maintained despite an unusually severe winter of 1983–84, 3 hurricanes in 1985, and marked differences in land use between years. That absolute density estimates of larvae as a function of host density agreed with observation further suggests that the projected densities in the model are realistic and provide increased understanding of the effect of host density on the population dynamics of this mosquito.

SUGGESTED AREAS OF ADDITIONAL RESEARCH

Further validation of WaterMod. Coefficients used in WaterMod were not developed by simulation to optimize the fit to the particular situation in Acadia; the algorithm uses only standard hydrological parameters and coefficients. As a result we expect, with appropriate inputs, WaterMod would do a fair job in other rice-growing regions with a shallow hardpan and clay soil. We would like to see additional hydrologic data sets developed from other areas to further evaluate WaterMod.

Estimates of survival. Better estimates of the effects of larval density, habitat type, and the nature and impact of predation on immature survival would be useful. Values used in simulation for immature survival in the DITCH/SWALE and NON-RICE habitats were not based on observations but were developed through simulation and discussion with several RMMP/S-122 researchers. Better estimates of survival in rice would also be useful. The model tends to overestimate adult production from late, first-crop rice. This may be due to any one of a number of factors, but without additional data, it is impossible to identify any particular variable. We suspect the overestimate, in part at least, is the result of not taking into account the role of agricultural chemicals which are more widely (exclusively?) used during the first crop (M. D. Andis, personal communication). More refined estimates of egg survival by diapause state and as a function of soil moisture and temperature, age, and predators would be useful.

Prediction of water temperatures. While McHugh and Olson (1982) observed a reduction in overall survival in the laboratory at temperatures outside a range of ca. 19–34°C, temperature was not included as a factor in determining active immature survival in PcSim because our estimated water temperatures as predicted by air temperatures fell within this range. However, we suspect that temperatures occasionally are

sufficiently high in shallow depressions of the NON-RICE and DITCH/SWALE areas (and perhaps RICE as well) to drastically limit larval survival. These higher-than-expected temperatures may be due to a lack of shading vegetation, dark bottom coloration, etc. Hence, we probably need predictors of water temperature in addition to air temperature. In addition, water temperature estimates permitting more precise immature development approximations would improve the ability to accurately predict larval mortality due to the habitat drying before emergence. Figure 9 presents predicted hatch-to-emergence times as predicted in PcSim. We are not aware of any systematic bias in these estimates, but reports for comparison are few and relate to the rice habitat only. The estimates in Fig. 9 vary considerably from day to day because each estimate is the expected overall development time, should the temperatures of that particular day remain constant throughout the development period of the larvae.

Spatial heterogeneity. In PcSim, because spatial heterogeneity is not considered, hosts are assumed to be uniformly distributed and only their density, as it affects adult survival, is considered to influence the population dynamics of *Ps. columbiae*. However, it seems clear from the literature cited by Focks et al. (1988a), that spatial distribution of *Ps. columbiae* is not random or uniform but contagious and, to a variable

degree depending on soil moisture conditions throughout the rice agroecosystem, associated with aggregations of primary host.

A number of factors produce this affiliation. Recently engorged *Ps. columbiae* females are poor fliers (Horsfall 1942), typically require multiple bloodmeals for the initial gonotrophic cycle, and do not need to commute to distant wooded daytime resting sites between meals but can remain in the low-lying vegetation in the immediate vicinity of the host (Edman and Bidlingmayer 1969). Moreover, cattle, in addition to providing a source of blood, create fresh hoofprints ideal for oviposition (Meek and Olson 1977), and their droppings, or bacteria associated with droppings, aids larval development (Al-Azawi and Chew 1959). We believe that this simplification does not compromise the model's ability to evaluate IPM strategies or simulate the population dynamics of *Ps. columbiae* on a parish-wide basis. Nonetheless, an accounting of spatial distributions may be necessary before the model could be used as a foundation for an expert system designed to provide real-time control recommendations for multiple areas within an abatement district.

POPULATION DYNAMICS

The dynamics of *Ps. columbiae* populations in the rice agroecosystem are influenced by a num-

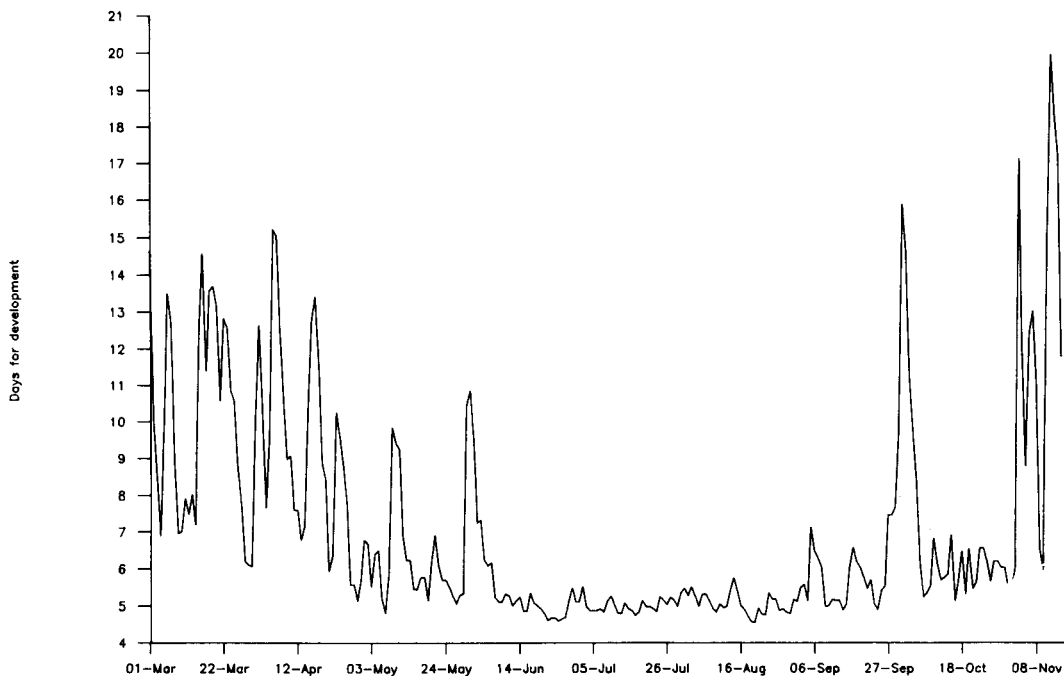


Fig. 9. Predicted overall development times of active immatures in Acadia Parish in 1984 as predicted by PcSim.

ber of environmental interactions which the model has demonstrated are not always easily understood or fully appreciated. This section presents an accounting of some of these interactions for the year 1984; the observations are based on insights gained from developing the models themselves and from simulation results in Acadia Parish.

The winter of 1983–84 was unusually cold with 2 occasions where temperatures remained below freezing for 3 or 4 consecutive days; minimum temperatures dipped to a low of -12°C . As a consequence, an unusually low proportion of eggs survived to begin the 1984 season (compare Fig. 5a with 5b).

The first adults in 1984 came from overwintering eggs in the DITCH/SWALE areas and from the area of NON-RICE which is not cultivated (see peaks labeled A in Figs. 5a and 10a); this hatch was a result of the first rain after April 1 (label A, Fig. 1a) when diapause was assumed to have terminated (J. K. Olson, personal communication). Notice that this rain hatched all eggs in NON-RICE (aa in NON-RICE panel of Fig. 5a) as eggs in this habitat are oviposited in the small surface depressions of the soil and very little surface water is required for inundation (Focks et al. 1988a). In contrast, the same rains brought off only those eggs in the lower elevations of DITCH/SWALE (aa in DITCH/SWALE panel of Fig. 5a), leaving the eggs higher up the slopes to be hatched later in response to a larger rain. Subsequently, these adults oviposited eggs on the pans and lower levee slopes of rice fields (A in RICE panel of Fig. 5a). Most rice fields at this time were being kept moist by flushes in the early phases of rice growth and a few were holding several inches of water in the process of seed bed preparation (A, Fig. 2a). Oviposition from this cohort did not occur in DITCH/SWALE or NON-RICE as these sites had become too dry (label aa, Fig. 1a). PcSim assumes that a small portion of overwintering eggs in RICE are not destroyed by cultivation the following year. These eggs (just barely visible and indicated by label aa in RICE panel of Fig. 5a) were still in diapause when initially inundated early in 1984 during seed bed preparation; they did not hatch at the end of the first week in April either as they were oviposited late in 1983 at elevations too high on the levees to be flooded by this particular rain.

The rain of early May in 1984 (B, Fig. 2a) raised water levels and hatched eggs in some rice fields, however, at this time, NON-RICE was devoid of eggs and the few eggs in DITCH/SWALE were too high to be inundated. The rain did temporarily raise soil moisture conditions (B, Fig. 1a) so that females coming from RICE as a result of previous additions of irrigation

water (B, RICE panel of Fig. 10a) could oviposit in all 3 habitats (B, Fig. 5a).

The first sizeable adult peak of the year (around May 29, label C in Fig. 10a) occurred in response to several rains around May 21 (C in Figs. 1a) which were sufficient to hatch eggs (C in all panels of Fig. 5a), not only in NON-RICE, but also from the higher elevations of DITCH/SWALE. RICE, continuing to produce low numbers of mosquitoes as a result of irrigation, produced additional adults in response to the temporarily raised water levels from rain (C in RICE panel of Fig. 10a). The gradual increase in area-wide egg densities continuing after May 21 was due to females coming from RICE; the subsequent sharper increase (cc, Fig. 5a) was a result of adults from the May 21 rain. The oviposition went into all habitats (between labels C and cc of all panels of Fig. 5a), as adequate soil moisture persisted from the time of hatch until after oviposition had begun. DITCH/SWALE stayed moist because the amount of rain was large (ca. 4" or 10 cm); WaterMod predicted maximum DITCH/SWALE depths of ca. 10" (25 cm). NON-RICE remained moist because several rains fell during this time and almost all RICE by this time was in permanent flood. Notice, however, after about May 31 (after cc in Fig. 5a), all areas except RICE were too dry for oviposition (cc, Fig. 1a) and as a result, the continuing oviposition from *Ps. columbiae* adults arising from water fluctuations in RICE occurred only in RICE.

Labeled D in Fig. 1a is a ca. 30-day period when frequent rains maintained water table depths near or above the surface. This was a period where *Ps. columbiae* egg densities tended to increase (especially in RICE, see D, Fig. 5a) from adults arising from all habitats. This regular growth, aided by warm temperatures and adequate moisture, was due primarily to the short time between oviposition and hatch resulting in multiple cohorts during a brief period of time. The relative gains in RICE over NON-RICE and DITCH/SWALE reflect: 1) the slight preference of RICE as an oviposition site over the other areas (Focks et al. 1988a), and 2) an accumulation of eggs in RICE which are not subject to inundation . . . the result of frequent oviposition on the upper portions of levee structures which are rarely flooded as spillways and irregularities in levee construction commonly limit maximum water depth. As discussed above, while light traps indicated the presence of adults during this time, the model consistently overestimated observed adult populations during this period (D, Fig. 10a).

After a break of ca. 14 days without rain, an interesting series of events around the end of the growing season of first crop rice began with

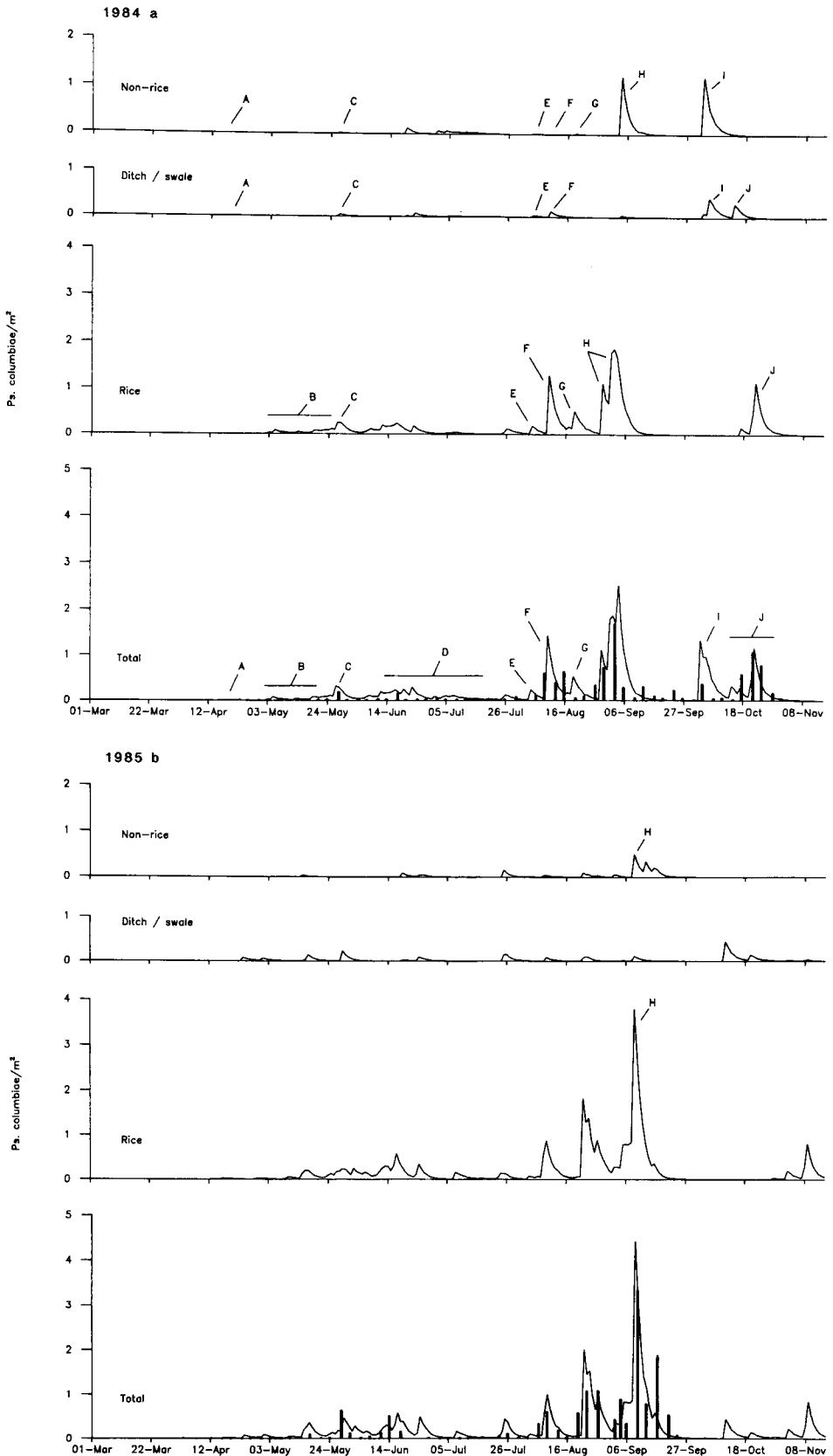


Fig. 10a and b. Predicted absolute densities of adults 1 or more days old by area of origin during 1984 and 1985 in Acadia Parish. Vertical bars in lower panels represent light trap data scaled by 0.0005 as in Fig. 4.

a modest rain on July 28 (ca. 1.4" or 3.4 cm). By this time, most rice fields had been drained prior to harvest (E, Fig. 2a). This rain hatched eggs at the lower elevations in DITCH/SWALE and RICE and virtually all of the eggs in NON-RICE areas (E, Fig. 5a). At the time, most eggs were in RICE and, as a result of recent full flood water levels, these were concentrated in a band at higher levee elevations. The resultant adult peak appeared in light trap collections on August 2 (E, Fig. 10a).

On August 4, Acadia Parish received ca. 6" (15.2 cm) of rain within a 24-hr period. Falling faster than fields could drain, water levels in RICE (still uncut) rose briefly to depths sufficient (F, Fig. 2a) to hatch only those eggs oviposited on lower levee slopes (F of RICE panel in Fig. 5a). Water levels in DITCH/SWALE (F, Fig. 1a) inundated virtually all eggs in this hydrologic area (F in DITCH/SWALE panel in Fig. 5a). Because of the paucity of eggs in NON-RICE as a result of recent hatch and incomplete development of subsequent eggs, NON-RICE areas contributed virtually nothing to the adult peak around August 9, (F, Fig. 10a).

About one week later, a few growers cut some very wet fields (ca. 20% of the rice acreage) and reflooded for a second crop with the aid of 3 small rains on August 10–12. This produced adults in light traps beginning August 19 from both RICE and NON-RICE areas (G, Fig. 10a). Cutting the balance of rice acreage was further delayed by the rains of August 10–12 (G, Fig. 1a) until August 21–24. The asynchrony of reflooding this acreage (some 80% of all first crop acreage) produced the adult peaks around August 29 and September 2 (H in RICE panel of Fig. 10a). Because RICE fields with cut levees behave hydrologically like NON-RICE areas, land which is not second-cropped is, for accounting purposes in PcSim, moved to the NON-RICE category and given a surface pond depth of 4" (10 cm) to reflect the deep tire ruts of harvesting equipment (see Focks et al. 1988a). Therefore, the large adult peak on September 3, shown graphically in Fig. 10a (labeled H in NON-RICE panel) as originating from NON-RICE, actually comes from first crop rice acreage which was not reflooded for a second crop; the date of the rain was September 29. In 1985, even though rice acreage was lower and, as a result a correspondingly higher proportion of all rice was reflooded, a NON-RICE peak at this time of the year is still evident from fallow rice (Fig. 10b, NON-RICE panel, label H).

It can be seen in Fig. 5a (label hh) that diapause eggs had begun to be oviposited by September 1 and that by around September 6, both diapause and non-diapause eggs were being oviposited in all hydrologic areas. Notice also dur-

ing the middle of September when there was no rain to cause hatch, that non-diapause eggs were declining in density faster than the newly-deposited diapause eggs, reflecting the greater survival of the hardier diapause eggs (see Focks et al. 1988a).

The rains of September 23–25 (I, Fig. 1a) hatched all non-diapausing eggs in NON-RICE and eggs at lower elevations in DITCH/SWALE (I, Fig. 5a) and produced a brood of adults which did not fully appear at light traps (I, Fig. 10a). Because a cold front passed through the area between September 30 and October 4 with low temperatures of below 5°C, the traps underestimated the actual size of the cohort. Because these temperatures are assumed not to be lethal, adults are reported in Fig. 10a at label I; these numbers are used to predict future oviposition, etc. However, Fig. 4a presents the expected adult light trap captures as a function of the population dynamics of PcSim (e.g., Fig. 10) as modified by low air temperatures and discussed in Focks et al. (1988a) (compare peaks at I in Figs. 4a and 10a).

The final event of the year reflects the results of a second major storm which dropped 10.5" (26.6 cm) of rain between October 6 and 23, 1984 (labels J in Figs. 1a and 2a). The previous rain (I, Fig. 1a) inundated all non-diapausing eggs in NON-RICE and the resultant females had deposited only diapausing eggs which were destined for 1985. This rain did hatch eggs in the DITCH/SWALE area. These eggs had been deposited high as a result of the high water levels from the 6" (15.2 cm) rain of the previous hurricane (F, Fig. 1a); these eggs had not been inundated by the smaller intervening rains of September 23–25 (I, Fig. 1a). The only area which had unhatched non-diapausing eggs after the rains of late October was RICE, as these eggs were located high on the sides and tops of levees and not subject to flooding. Adults from these rains were responsible for what is probably an unusually high number of diapausing eggs; as a consequence of this and a mild winter between 1984 and 1985, *Ps. columbiae* began 1985 with higher numbers than average.

While we could continue with a description of 1985, the preceding is hopefully adequate to provide an appreciation for some of the interactions between hydrologic and weather events and the population dynamics of *Ps. columbiae*.

DISCUSSION

Why does the rice agroecosystem support such unusually high densities of *Ps. columbiae*? The answer lies in the interaction of the biology of this flood-water mosquito with the modified environment associated with rice culture. In the

typical habitat as unmodified by man, the life history strategy of *Ps. columbiae* permits the almost exclusive exploitation of a short-lived and therefore usually predator-free larval habitat. Disadvantages associated with this strategy, of course, are the requirement of rapid immature development and the burden of egg attrition between floodings. The cost of the unusually rapid development in this mosquito is females with low energy and protein reserves. This in turn necessitates bloodmeals immediately after emergence for survival, as well as for oviposition.

Certain features of the rice agroecosystem discount some of the liabilities associated with this life history strategy. First, most rice in this country is grown where land is flat and a relatively shallow hardpan exists, factors which reduce costs associated with levee construction and irrigation, respectively. The environmental modification associated with the rice system introduces additional physical relief into this flat environment and it also provides a more steady source of moisture. These areas, e.g., seepage areas, levees, vehicle tracks, and irrigation and drainage ditches (which are often not disturbed and therefore aid in the overwintering of eggs), are critical elements of the modified environment. Rice levees provide almost continuous sites for oviposition, and, whether from irrigation or rainfall, water level increases here almost always persist long enough to permit emergence. Because all land in the rice agroecosystem is not suitable for rice or other crops, cattle are invariably introduced to put marginal land into productive use . . . a practice that, in addition to the creation of hoof prints for oviposition, provides the blood necessary to support *Ps. columbiae*, and droppings to encourage larval development. In conclusion, we find that the mosquito problems of this environment are largely the consequences of mans' activities.

The final paper of this series (Focks et al. 1988b) will present an evaluation of various current and proposed management strategies for this mosquito in the rice agroecosystem.

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