ARTICLES

COMPUTER SIMULATION OF MANAGEMENT STRATEGIES FOR *PSOROPHORA COLUMBIAE* IN THE RICE AGROECOSYSTEM[1]

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ABSTRACT. Various control strategies were evaluated using a previously-described and validated (Focks et al. 1988a, 1988b) simulation model (PcSim) of the population dynamics of *Psorophora columbiae* breeding in the rice agroecosystem.

As expected from field experience, focally-applied ground or aerial ULV aerosols of insecticides were seen to provide local control of peak populations. Similar control was predicted for larvicides when also used in and around urban and suburban areas. Both of these measures were predicted by simulation to provide only short term control of adults as a result of immigration of adults from surrounding, untreated areas. Evaluations of the effectiveness of diapause egg control or the elimination of early spring broods to provide lasting, season-long suppression were not encouraging if only conventional methods such as insecticides or tillage were used. This was primarily because the ability of *Ps. columbiae* to recolonize treated areas during the course of a breeding season would require the treatment of prohibitively large, parish- (i.e., county-) sized areas. Evaluations of host management (either removal or residual insecticide treatment of cattle) in and around urban and suburban areas were more encouraging. This technique, by providing continuing pressure on populations, has the potential to offset the impact of immigration and thereby afford long-term suppression in local areas. Finally, evaluations of the impact of modifications to irrigation practices indicated that this approach warrants consideration as a supplemental control technique.

These results suggest that field evaluations of model predictions would be useful. They emphasize the need to better understand the movement and spatial distribution of *Ps. columbiae*. These factors would bear directly on the cost and therefore, the practicality of several of the long-term suppression strategies evaluated as they determine the size of the treatment area surrounding population centers needed to offset the impact of immigration from surrounding, untreated areas.

INTRODUCTION

For the past 10 years, the rice agroecosystem and its associated mosquitoes have been the topic of a comprehensive research effort focused on the development and implementation of integrated pest management (IPM) strategies. In previous papers (Focks et al. 1988a, 1988b), we reported the development and validation of simulation models of the key elements of this system that are known to influence the population dynamics of *Psorophora columbiae* (Dyar and Knab).

The rationale for the construction of these models was to summarize current knowledge of the system, assist in the identification of areas where additional research efforts would be warranted, aid in the understanding of the population dynamics of *Ps. columbiae* through computer simulation, and facilitate the evaluation and optimization of current and proposed IPM strategies for this mosquito. This final goal is the subject of the present paper.

For earlier accounts and summaries of individual control techniques for *Ps. columbiae*, see Anonymous (1967), Horsfall (1942, 1955), Schwardt (1939), and Olson (1979); for an international perspective, see Tsutsui (1984).

RAMIFICATIONS OF THE LIFE HISTORY STRATEGY OF *PS. COLUMBIAE*

Biological systems are obviously complex. They are usually non-linear, being under the influence of a host of various types of feedback and other control mechanisms. We begin our analysis of suppression methods for *Ps. columbiae* with a brief discussion of life history strategies which will allow parallels and conclusions so be drawn regarding *Ps. columbiae* control from the wealth of information on other insect

IPM systems (see Service 1985). Good coverage of this topic may be found in a study guide by Wilson and Bossert (1971).

As an aid to understanding the dynamics of living systems, MacArthur and Wilson (1967) suggested that the life history of organisms may be classified on a continuum ranging between so-called "r-strategists" and "K-strategists" where the parameters r and K refer to the intrinsic rate of increase and the carrying capacity of the environment under stable conditions, respectively.

K-strategists tend to be found in stable environments where selection places a premium on their ability to compete on a long-term basis with other organisms which are also at densities approaching the carrying capacity of the habitat. Typically, key mortality factors include those which operate in a density dependent manner. An example is the tsetse fly. In contrast, r-strategists are typically short-lived with high growth rates and migratory behavior. These characteristics enable them to rapidly colonize and utilize ephemeral resources. The housefly is a good example of an r-strategist. In many instances, it appears that there are no density-dependent mortality factors regulating r-type populations. Key mortality factors include include catastrophic density independent events such as freezing, desiccation, etc., from which they are well equipped to recover due to their extremely high growth rates.

Another concept, that of controlling vs. regulating mortality factors should be mentioned. Varley (1963) suggested that a factor "controls" when it causes a change in the size of a population but does not have a stabilizing influence. Such factors, e.g., weather, insecticides, etc., often act in a density independent fashion: the degree of mortality is independent of the size of the population. In contrast, "regulating" factors, usually acting in a density dependent fashion, serve as feedback mechanisms dampening oscillations in population size. For Ps. columbiae, examples of such regulatory or feedback factors include larval density and host animal abundance (Focks et al. 1988a).

It is obvious that Ps. columbiae has many of the attributes of an extreme r-strategist: High fecundity and short and multiple generations are characteristic. Flight ability allows the rapid discovery and colonization of an ephemeral habitat, the rapidly-drying pond. A high growth rate allows the rapid utilization of resources before other competing organisms can exploit the habitat. Key factors influencing short-term population dynamics such as weather, and in the rice agroecosystem, agricultural practices are largely density independent (Focks et al. 1988a). However, provided substantial rice production con-tinues, host abundance (a density dependent factor) is clearly the primary determinant of long-term, average population levels of Ps. columbiae in Jefferson Davis and Acadia parishes (i.e., counties), Louisiana. At the host densities observed in these parishes, immature abundance is usually too low to be adversely affected by density dependent larval mortality (see Fig. 6, Focks et al. 1988b, Fig. 3, Focks et al. 1988a, and Andis and Meek 1985).

SIMULATION METHODS

In the studies described herein, the impact of various control methods on Ps. columbiae was evaluated by comparing density trends of an untreated population with trends in a treated population as predicted by computer simulations using PcSim, a comprehensive model of population dynamics (Focks et al. 1988a, 1988b). Simulations were begun using the number and distribution of overwintering eggs resulting from equilibrating PcSim for 6 simulation years using a nominal weather pattern (Focks et al. 1988b). Values for parameters such as land use, planting dates, weather, etc., were based on the situation in Acadia and Jefferson Davis parishes located in southwestern Louisiana during 1985. Because the impact of local control efforts, e.g., ultra-low volume (ULV) applications for adult control in and around urban and suburban areas, would be influenced by the immigration of Ps. columbiae from surrounding and untreated areas during the course of a season, PcSim, as used here, describes the population dynamics of a parish-sized area.

In recent years, heavily populated urban areas in Jefferson Davis parish have commonly received between 10 and 16 adulticide applications during each mosquito season (J. S. Billodeaux, personal communication). Simulation results indicate that when spray operations are triggered by an adult density of 2.8 or more per square meter, 12 treatments per year would be applied. When simulating the results of some control method(s), monitoring the number of times the model's population exceeded this 2.8/m^2-threshold provided an index for comparison between treated and untreated populations or among populations treated with different strategies. In some instances, comparisons of control effectiveness were also made on the basis of average annual densities of eggs, larvae and pupae, and/or adults.

SIMULATION RESULTS

Adulticiding. Much work has been directed toward the evaluation of new toxicants, and application and evaluation methods for Ps. co-

lumbiae control (Dowell 1965, Taylor and Rathburn 1970, Mount et al. 1972, Meisch et al. 1973, Coombes et al. 1977, Roberts et al. 1980, Meek and Billodeaux 1982, Walker et al. 1981). Currently, the Jefferson Davis Mosquito Abatement District (JDMAD) applies ULV aerosols of several types of adulticides by ground truck and fixed-wing aircraft. Unpublished data suggest an average mortality per treatment of 80 and 95% for ground and aerial applications, respectively (J. S. Billodeaux, personal communication). Used primarily in urban and suburban areas, the value of mosquito adulticide stems from providing temporary relief from high adult populations; they are not applied with the intention of affecting the population dynamics of *Ps. columbiae* on a long-term basis either locally or on a parish-wide basis. As such, applications are applied focally on municipal areas which comprise ca. 15% of the land area of the parish.

Figure 1 presents the impact of 12 adulticide applications throughout the year as simulated by PcSim. In the treated area (15% of total land area), insecticide-related mortality was assumed to average 90% on the day of application. Each

spray was triggered in response to the hypothetical population exceeding the 2.8 adults/m^2-threshold. While landing rates of *Ps. columbiae* within sprayed areas are often reduced to zero prior to reinvasion (J. S. Billodeaux, personal communication), on a parish-wide basis (the area simulated by PcSim), repetitive applications influenced the overall population dynamics of *Ps. columbiae* very little. This is almost entirely the consequence of the limited application area. The untreated population exceeded the threshold 17 times.

Figure 2 contrasts the untreated population with predicted populations resulting from either 1) a single, parish-wide application directed against the largest adult peak of the simulated year which occurred on September 2 in response to reflooding for the second crop or 2) three parish-wide treatments triggered by exceeding the 2.8 adults/m^2-threshold. The single parish-wide treatment, while having the immediate impact one would anticipate, resulted in no long-term reduction, reflecting both the high growth rate of this pest and the relatively small proportion of the population that is in the adult form
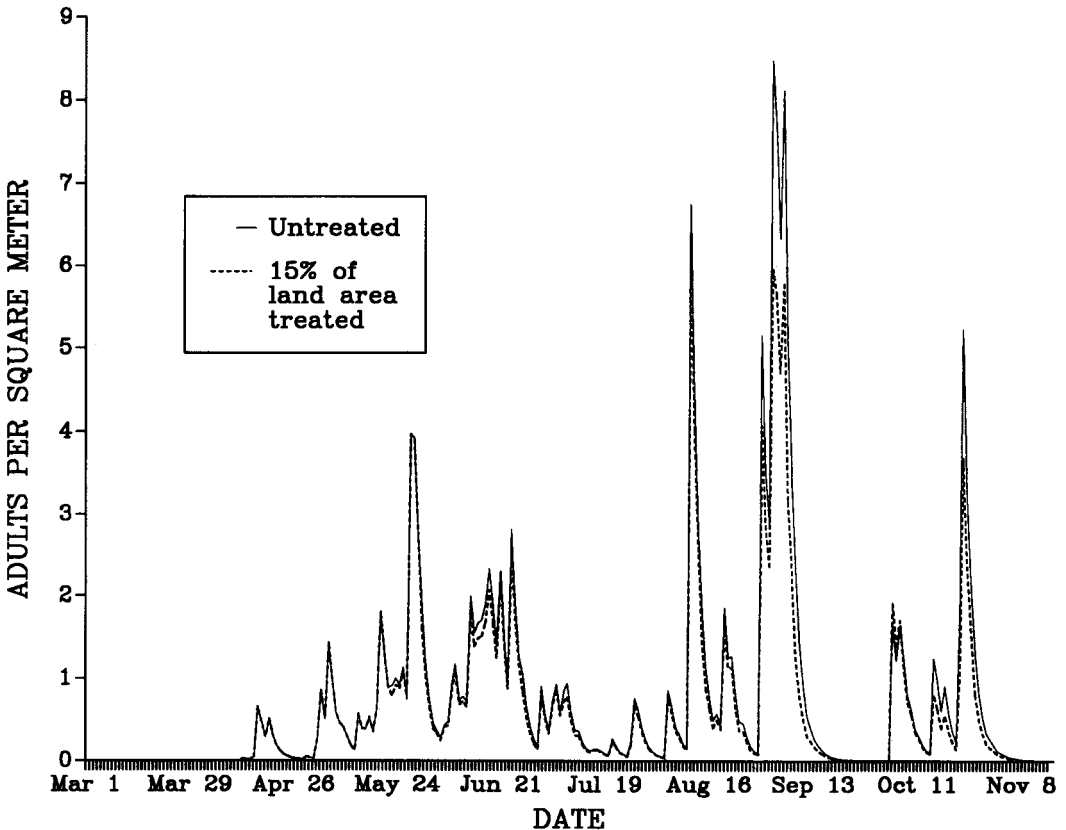

Fig. 1. Comparison of the seasonal trends of an untreated adult population of *Psorophora columbiae* with a population focally treated 12 times during the year with an ULV aerosol of adulticide causing a 24-hr mortality of 90%. Proportion of land area treated was 15%.

at any particular time and thereby amenable to control with an adulticide (cf., adult, egg, and larval densities in Figs. 4, 5,and 6 in Focks et al. 1988b). However, multiple and properly timed adulticide applications across the entire parish reduce oviposition to a degree sufficient to bring about a substantial reduction in average, season-long adult densities (ca. 0.75 and 0.30 adults/m^2 for untreated and treated, respectively).

Aside from the important issue of resistance development, logistical and cost considerations make a parish-wide suppression effort based on adulticide questionable. The efficacy shown in Fig. 2 is predicated on the ability to time all sprays to occur while peak populations are still nulliparous, i.e., effectiveness stems from the prevention of oviposition. Typically, during the summer, the asynchrony of emergence throughout a parish in response to local showers, unsynchronized flooding, etc., results in many local and asynchronously-developing subpopulations. Locating and treating these widely distributed subpopulations at the proper time would be impossible in any large-scale operation.

In summary, adulticides act as a density independent influence serving to control (in contrast to regulate) Ps. columbiae populations. Given the limited area and frequency of application, the model indicates that, as currently practiced, treatment throughout the year is not accompanied by significant rebound from a relaxation of any of the density dependent mortality factors in the system. It is obvious that focal ULV adulticide applications provide important, albeit understandably transient, control of pestiferous levels of adults. It is likely that in any type of integrated suppression strategy, adulticide will continue to be a principal technique for reducing peak adult populations in urban and suburban areas. Until long-term suppression strategies become available, adulticide will continue to be the method of choice for Ps. columbiae control. Because of cost, the threat of resistance, and the difficulty of timing sprays to hit peak adult populations which develop asynchronously throughout the parish, adulticiding is probably best used as a focal treatment.

Larviciding. The evolution of larvicidal methods has paralleled the development of adulticide capability for the control of Ps. columbiae. For a comprehensive bibliography see Paine (1983). Compounds evaluated range from DDT and parathion to insect growth regulators to surface films to various strains and species of Bacillus. Application methods vary from preflood treatment to point-source introduction to aerial and ground application of aerosols and granular materials. Like adulticide applications, larvicides act in a density independent fashion and serve to "control" populations.

Larvicides are not the mainstay of control programs in districts like JDMAD where the primary pest is Ps. columbiae; this is in marked contrast to districts where the important problem species are permanent-water breeding mosquitoes such as Anopheles quadrimaculatus Say and Anopheles crucians Weidemann. In southwestern Louisiana, Ps. columbiae breeds in a variety of habitats in and around numerous population centers: In addition to rice fields where populations are principally subject to irrigation, breeding occurs in diverse, typically small, and widely dispersed habitats such as pastures, soybean fields, and roadside ditches. These additional non-rice and ditch/swale sites of Ps. columbiae production are asynchronously flooded by rainfill which, of course, is unpredictable and not evenly distributed throughout the district. Because of these factors, with the exception of rice fields, the effective use of larvicides in all of the habitats used by Ps. columbiae would be contingent upon timely, continuing, comprehensive, and therefore, on a large-area basis at least, prohibitively expensive surveillance. As a result, larviciding has principally been confined to controlling the emergence of Ps. columbiae associated with reflooding of second crop rice within a few miles of population centers.

Recently, JDMAD has been using a system to introduce a suspension of Bacillus thuringiensis israelensis (de Barjac) (Bti) into irrigation water used to reflood harvested rice fields (McLaughlin and Vidrine 1984). Usually, Ps. columbiae populations associated with the second crop are some of the largest of the year (J. S. Billodeaux, personal communication and Focks et al. 1988b). In simulations of the efficacy of Bti used in this manner, we have assumed that parish-wide, Bti application to second-cropped fields resulted in an average 3rd- and 4th-instar mortality of 61%. This value reflects the inability to treat all fields and the results of partial treatments due to irregularities in irrigation practices (see McLaughlin and Vidrine 1984 for details). Figure 3 compares treated and untreated adult populations as predicted by simulation. While the reduction in the major peaks associated with reflooding are obvious, because of the limited treatment area (typically, less than complete coverage of only rice acreage), the single application, the high potential growth rate of Ps. columbiae, and the fact that only a low proportion of the total population exists at any particular time in the larval stage, little lasting impact subsequent to treatment is realized.

Where the untreated adult population exceeded the threshold 17 times, the Bti-treated population exceeded it 12 times. If ULV is combined with the use of Bti (as presented in Fig. 3), simulation indicated that 9 applications
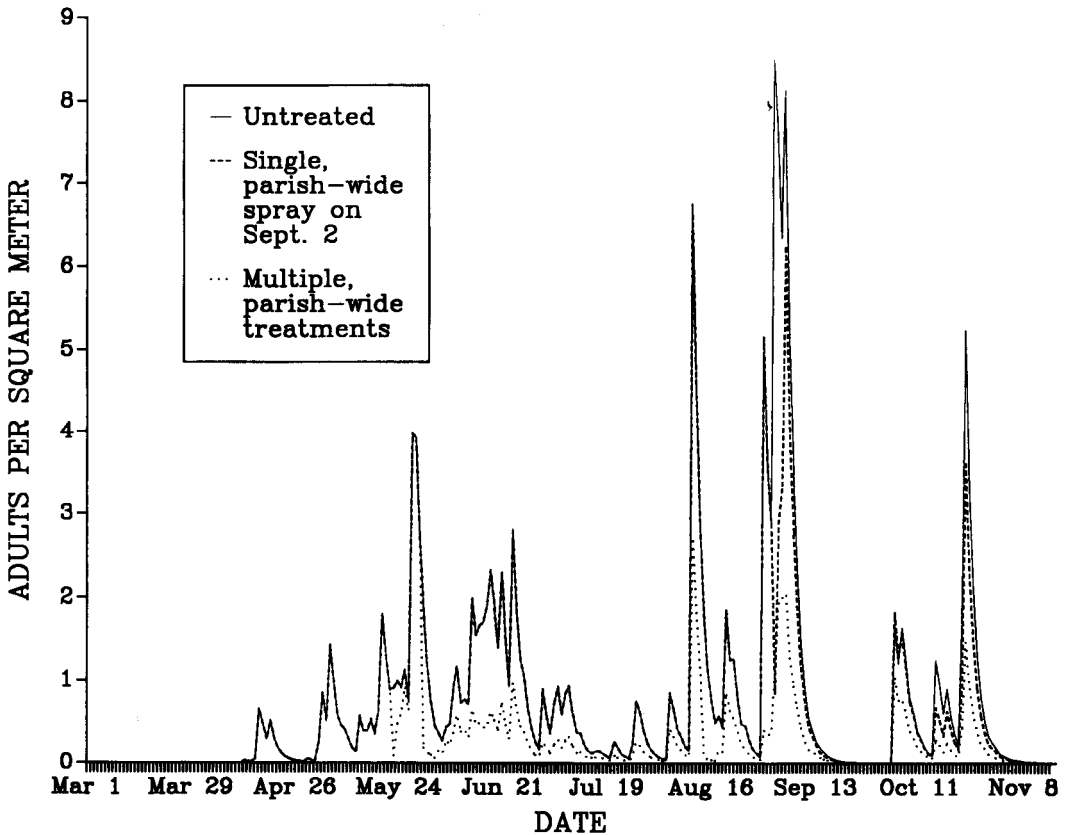
Fig. 2. Comparison of the seasonal trends of an untreated adult population of *Psorophora columbiae* with populations receiving either single (on September 2) or multiple (May 22, May 30 and August 13) parish-wide treatments with an ULV aerosol of adulticide causing a 24-hr mortality of 90%.

would be required, i.e., the use of *Bti* results in a savings of ca. 3 applications over a strategy of ULV alone. This is likely an unduly pessimistic assessment: a reduced adult population, while still requiring adulticide, may justify the cost of larvicide on the basis of reduced landing rates.

In years without rainfall during the reflooding period, i.e., periods when virtually all *Ps. columbiae* originates from rice, the use of *Bti* adjacent to population centers in this fashion usually provides, similar to adulticide, effective but temporary relief (J. S. Billodeaux, personal communication). The cost advantages may disappear if inadequate coverage of rice acreage or rainfall-induced broods require supplemental adulticide applications.

With area and therefore cost increasing roughly with the square of the radius of the area to be treated, the major unanswered question, of course, concerns the optimum size of the treatment area around a town which would balance increasing costs with reduced immigration of adults from outlying, untreated areas. Given the distribution of *Ps. columbiae* among several habitats (practically speaking, only some of which

are amenable to larval control efforts) and the potential for adult movement (see Focks et al. 1988a), the rationale for larval control efforts for this species seems uncertain. Of the 35 or so papers on larval control of *Ps. columbiae*, not a single study deals with the relationship between larvicidal efforts and subsequent pest levels of adults. Is the relationship so obvious as to not require comment or does the topic warrant some examination?

The above reservation aside, we suspect that the statements made for the place of adulticide in the control of *Ps. columbiae* are appropriate for lavicidal efforts as well: In line with current practices, it would appear from these studies that larviciding has a place in focal control efforts in an around urban and suburban areas. Its role in an integrated suppression effort is less clear.

A final comment on larvicides concerns agricultural chemicals: It is undoubtedly true that these compounds, used primarily during the first crop, decimate predator populations and result in higher mosquito populations (see for example Chambers et al. 1979, Service 1977, and Alex-
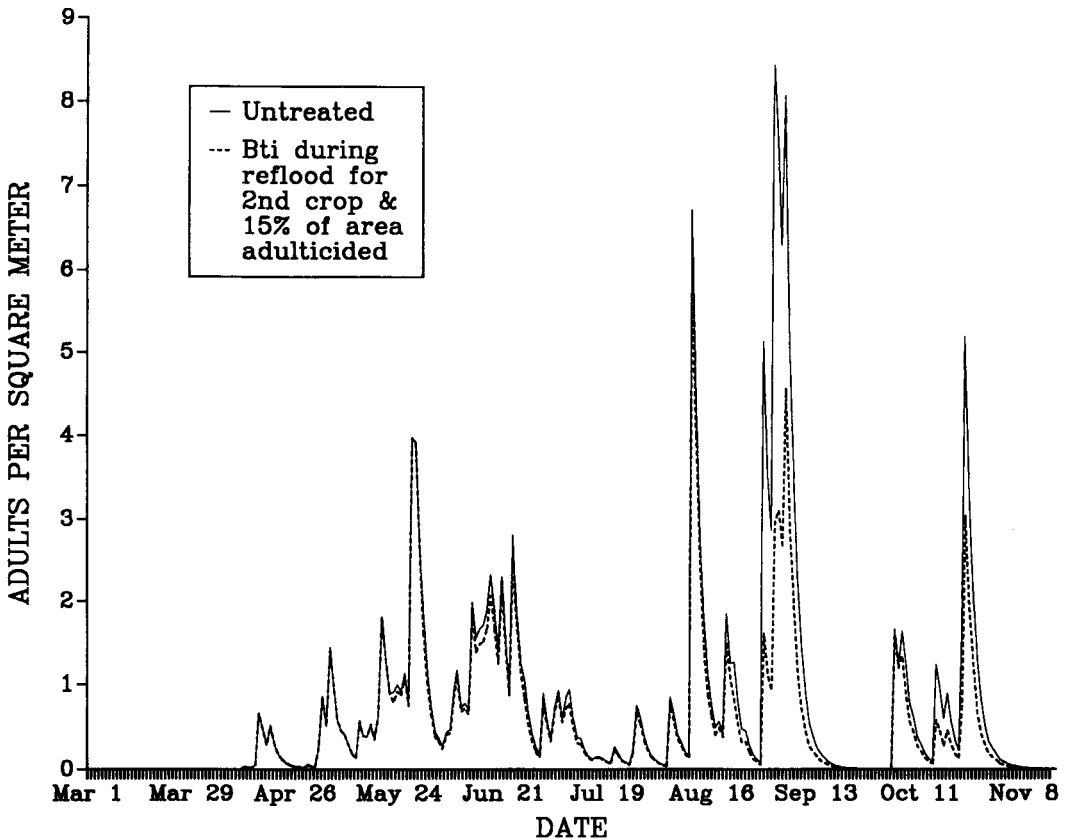
Fig. 3. Comparison of the seasonal trends of an untreated adult population of *Psorophora columbiae* with a population resulting from the treatment of irrigation water with a suspension of *Bti* at the time of reflooding for second crop and focally-applied ULV adulticide as in Fig. 1.

ander et al. 1982). Given the damage that non-selective compounds (whether directed against mosquitoes or rice pests) have on non-target beneficial insects and the importance of predators as the key mortality source of *Ps. columbiae* larvae and pupae (Andis and Meek 1985) in rice fields, can the use of mosquito larvicides other than very specific ones like the *Bacillus*-based materials, etc. be justified? Alternatively, given the widespread and frequent use of agricultural chemicals, would any significant additional damage result from the use of a non-selective and less-expensive compound by mosquito abatement personnel?

Control of diapausing eggs. As an overwintering mechanism, the history strategy of *Ps. columbiae* in temperate regions includes the deposition of diapausing eggs.[2] As a long-term suppression method, Delorme et al. (1987) and

others have proposed a scheme involving the reduction of overwintering eggs via cultural practices or the elimination of females depositing them in the fall.

At the latitude of southern Louisiana, the proportion of diapause eggs typically increases from 0 to 100% during September in response to temperature and changing photoperiod (Delorme et al. 1987). As hatch ceases during early November (J. K. Olson, personal communication), measures to eliminate females destined to produce diapausing eggs would have to be conducted during September, October, and early November. Alternatively, egg destruction via tillage could be accomplished anytime between mid-November and the following March or early April prior to the first brood.

Figure 4 presents simulated adult populations when the percentage of diapause eggs killed range from 0 to 80%. The number of times a population exceeds the threshold of 2.8 adults/m^2 when 40 and 80% of all diapausing eggs are eliminated during the previous season by either method is 11 and 6, respectively; these correspond to reductions of 35 and 65% when com-

[2] Delorme, D. R. 1984. Egg diapause in *Psorophora columbiae* (Dyar and Knab): Development of a predictive diapause induction model. Unpublished Ph.D. Dissertation, Texas A and M University. 95 p.
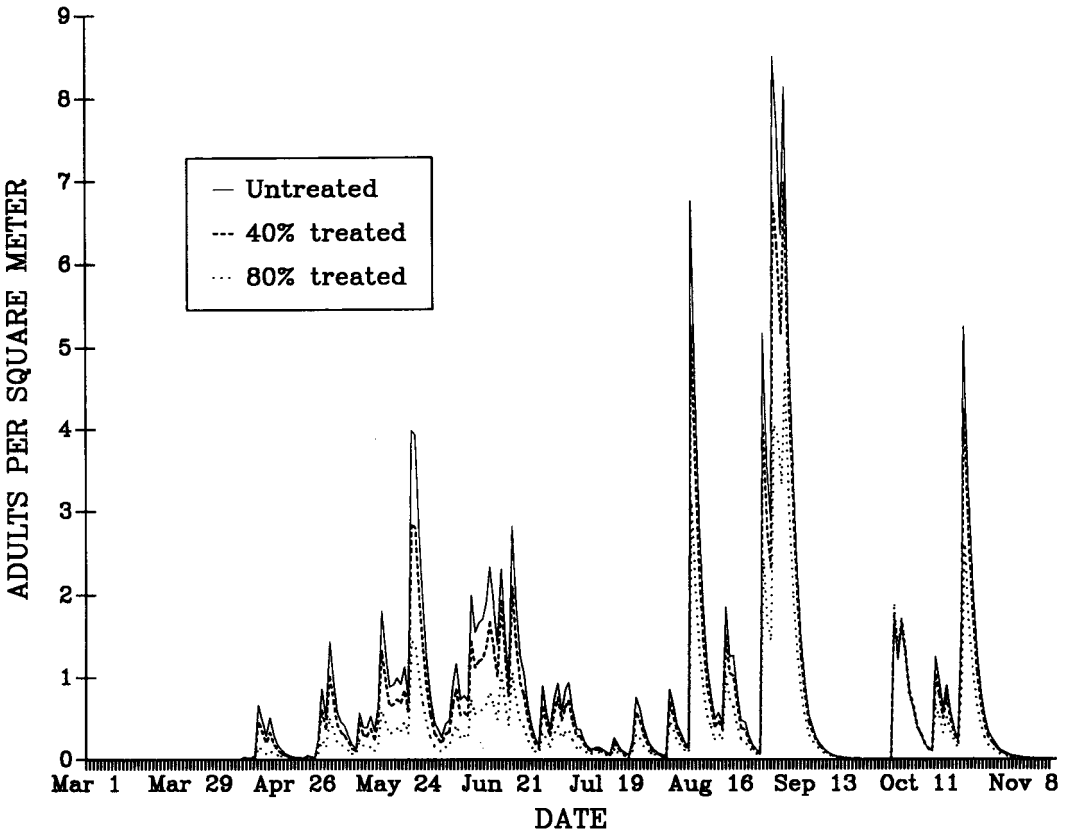
Fig. 4. Comparison of the seasonal trends of an untreated adult population of *Psorophora columbiae* with populations resulting from the elimination of 40 and 80% of diapausing eggs prior to the first hatch of the season.

pared to the untreated population which exceeds the threshold 17 times. The cost and impracticality of diapause egg control aside (see below), the lack of appreciable success even with high proportions of egg elimination is perhaps surprising. Simulation results suggest that properly-timed parish-wide adulticiding during the early summer months (see Fig. 2) would be expected to be more effective. The strong ability of *Ps. columbiae* to rebound, however, is understandable in light of the high short-term growth potential and ability to recolonize depopulated regions of this largely r-type species.

Figures 4 and 5 in Focks et al. (1988b) illustrate, from field and simulation data, the ability of *Ps. columbiae* to recover rapidly from catastrophic reductions in population size. The winter of 1983–1984 was unusually cold and as a consequence, an uncommonly low proportion of eggs (perhaps only 10 to 20%, see Fig. 7 in Focks et al. 1988a) survived to begin the 1984 season. Notice, however, that while adult populations were unusually low early in the season of 1984 (compare Figs. 4a with 4b, adult densities in 1984 and 1985, respectively), by mid-season, an

almost full recovery had occurred (cf. Figs. 5a and 5b, egg densities for the same years).

In summary, we would not expect a diapause egg control program (based on ULV or tillage) to be the most cost-effective suppression strategy for 3 reasons: First, given that perhaps two-thirds of all control efforts are normally required after mid-August (J. S. Billodeaux, personal communication), it would be difficult to justify the cost of a diapause control program on the early-season savings alone. Should this be the case, substantial, season-long suppression would be required to amortize program costs. As *Ps. columbiae* would almost certainly recolonize an urban-sized area during the 8 or 9 months that it is active each year, a diapause program would necessarily involve the treatment of rather large (county-sized, or in the case of Louisiana, parish-sized?) area. Second, this type of program would be difficult because killing diapause egg-laying females or their eggs on a parishwide basis would be difficult. The fact that diapause egg-laying females emerge over the course of 3 or 4 weeks would make their control even more expensive than the occasional, parish-wide ULV
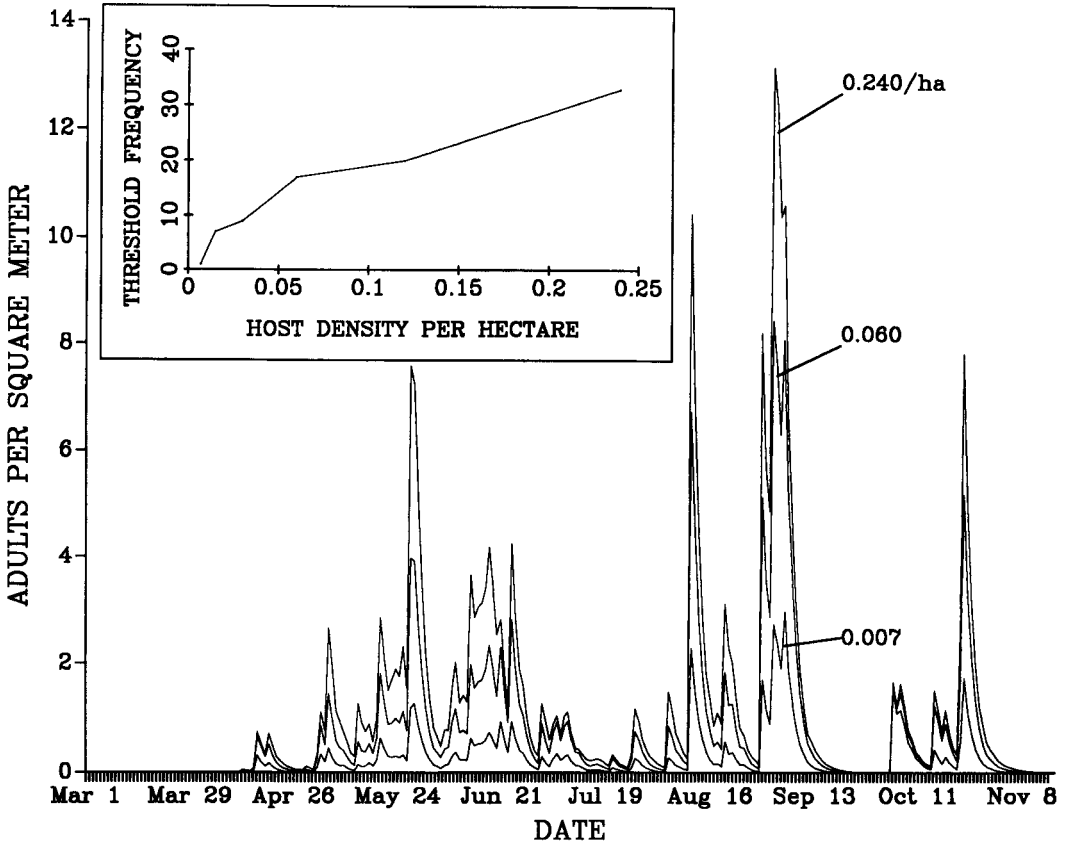
Fig. 5. Seasonal trends of *Psorophora columbiae* adults as a function of large-animal host density. Insert presents the frequency with which populations in equilibrium with various host densities exceed the 2.8 adults/m^2-threshold during the year.

discussed previously. Alternatively, a single, parish-wide brood resulting from a heavy, area-wide rain would be difficult to spray in a timely fashion with the limited resources of a mosquito abatement district. To kill diapausing eggs in the spring is also problematic: most eggs are already killed with current tillage practices (see Focks et al. 1988a, 1988b) with the balance normally coming from ditch/swale areas and non-cultivated areas (Schwardt 1939, Horsfall 1942). These overwintering egg sites, widely distributed and not normally tilled, are therefore difficult (if not impractical) to control. The third reason is that the high growth rate of *Ps. columbiae* would likely result in sufficiently high populations by late in the season so as to require conventional control efforts.

Early spring adult control. This method is essentially another method aimed at "nipping the population in the bud" and thereby preventing or delaying subsequent populations. In one case, you eliminate the eggs destined to produce the spring brood and in the other, you attempt to kill the adults arising from these same over-wintering eggs. The remarks and reservations regarding diapause egg control are appropriate here as well.

Of the methods discussed here, programs involving the control of diapause eggs or early spring adults to achieve season-long suppression of *Ps. columbiae* are the only cases where we envision the technique as (necessarily) encompassing a large, if not parish-sized area. With other techniques, we envision control methods confined to the area in and around urban/suburban areas because either 1) the goal is short-term control and immigration is not considered of major importance (e.g., adulticide or larvicide), or 2) more long-term suppression via measures where the continual pressure of the technique controls immigrants as well as local populations (e.g., host management, discussed below).

Host management. As indicated in Focks et al. 1988a, large-animal abundance is the primary determinant of long-term, average population levels of *Ps. columbiae* in the rice agroecosystem as the availability of hosts influences both fe-

cundity and adult survival. This influence is a density dependent and regulating factor (McLaughlin and Vidrine 1987, Focks et al. 1988b). Data were presented in the validation of PcSim (Focks et al. 1988b) to indicate that both larval densities in second-cropped rice fields and average light trap captures could be predicted as a function of nearby large-animal host densities.

Figure 5 presents simulated population trends of *Ps. columbiae* adults as a function of large-animal host density; the insert in this figure displays the frequency with which adult populations in equilibrium with these various host densities would have been sprayed in response to exceeding the 2.8 adults/m²-threshold during the year. For reference, the density of cattle (the primary, large-animal host) in Acadia parish, LA during 1984–86 was 0.06/ha (Focks et al. 1988b). Decreases in simulated host densities to levels below those found in southwestern Louisiana (ca. 0.06 cattle/ha) are accompanied by significant reductions in the frequency of exceeding the spray threshold. For example, reducing large animal density by 50% to 0.03/ha would roughly halve the number of times a population would have to be treated with adulticide.

These results are certainly encouraging. The efficacy seen here stems from altering the systems ability to produce high densities of *Ps. columbiae*, i.e., suppression. It is in marked contrast to control efforts aimed at killing the occasional high peak of emergence. Notice that the long-term suppression of populations via host management would significantly reduce overwintering egg densities and thus the subsequent spring population, i.e., host management, or any other tactic for that matter, could constitute an egg-diapause control program with attendant impact in subsequent years. While the magnitude of movement of *Ps. columbiae* would obviously affect the practicality of this method, it certainly suggests that the practice of grazing cattle in urban area which in turn are surrounded by rice fields is expensive from the stand point of mosquito control.

The relationship between host density and the frequency of exceeding the threshold is nonlinear at relatively high or low host densities for 2 reasons: First, as host densities increase, immature densities become high enough to progressively come under the influence of density dependent mortality, a factor which is normally not limiting at lower host densities. The result is that higher animal densities are not accompanied by corresponding increases in mosquito abundance, Secondly, at very low or very high average populations, the majority of peaks are either below or above the fixed threshold. As a result, going increasingly lower or higher does not continue to decrease or increase the frequency with which the threshold is or is not exceeded. Populations of *Ps. columbiae* at large-animal host densities approaching zero do not disappear because of the presence of suitable, smaller animals and, under these conditions, the model projects that *Ps. columbiae* would not be a major pest.

Treatment of large-animal hosts with residual insecticide. Kuntz et al. (1982) suggested that insecticide-treated cattle could serve as "killing agents" for *Ps. columbiae*. With this in mind and as a result of simulations with PcSim reported below, McLaughlin et al. (1989) determined the efficacy of permethrin as a residual adulticide on cattle. Their results indicated that either a water-based, whole animal spray or an oil-based pour-on would initially kill 80–100% of all host-contacting *An. quadrimaculatus*. At 7 days post-treatment, mortalities declined to ca. 55% and then to ca. 25% at 14 to 21 days. Similar results were also observed by J. K. Olson (unpublished data) with this insecticide and *Ps. columbiae*.

Figure 6 contrasts the untreated population with populations where various proportions of the cattle were treated every other week with permethrin using the residual mortalities given above. The insert in this figure presents the frequency with which these treated populations would have exceeded the 2.8 adults/m²-threshold during the year.

Simulations with PcSim suggest that this method could be promising and should be pursued. The effectiveness stems from persistently attacking the system at a critical point, that of adult female survival and hence fecundity. As all females must take bloodmeals multiple times prior to the first gonotrophic cycle (see Focks et al. 1988a for references) and a high proportion of blood-feeding (>85%) occurs on cattle in this environment, the method introduces a restraining influence which cannot be adequately compensated for elsewhere in the system. Assuming some degree of movement between blood meals, even at low treatment rates, the method influences virtually all females in the system because multiple meals are required. As a result, the treatment of the principal host in this system with a residual toxicant results in the exposure of a substantial proportion of the adult population. This is in marked contrast to the occasional and infrequent treatment of only small portions of the total population as in the case of larviciding or adulticiding.

Questions of the practical feasibility aside, given the (apparently) limited movement of *Ps. columbiae* (see Focks et al. 1988a), the results shown in Fig. 5–6 strongly argue that some type of host management be given consideration in the development of any bona fide integrated population suppression strategy. Strategies
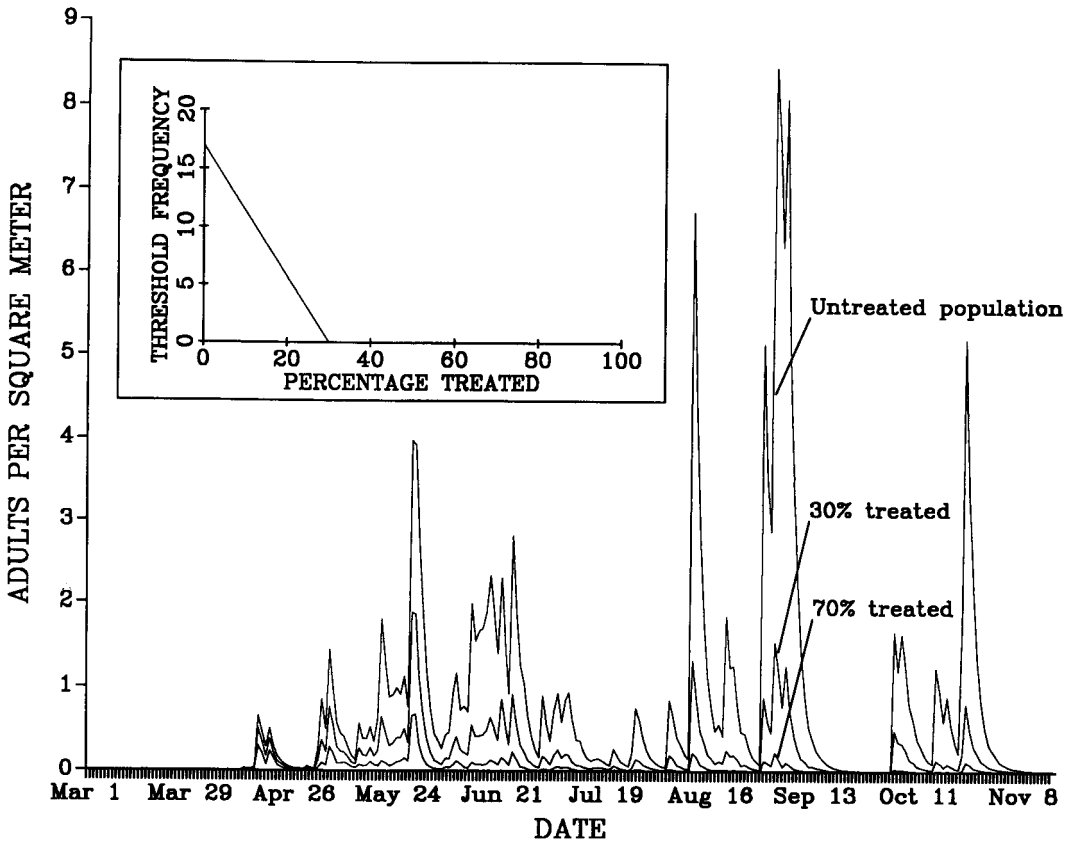
Fig. 6. Seasonal trends of *Psorophora columbiae* adults as a function of the proportion of cattle treated every other week with a residual insecticide. Insert presents the frequency with which populations subject to various proportions treated with a residual insecticide every other week exceed the 2.8 adults/m^2-threshold during the year.

could include the incorporation of large animal treatment with a residual insecticide and/or their exclusion from urban areas combined with standard insecticidal measures as necessary. A caveat however, is that to the degree that large-scale movement is the rule for this species, the practicality of this method would be expected to decline as treatment or elimination of large animals would be required from increasingly larger areas around each population center. Demonstration of the effectiveness of this approach, whether practical operationally or not, could promote and influence discussions on topics such as who should pay for mosquito control, whether zoning changes would be appropriate, etc.

Changes in land use. The proportion of land planted to rice each year changes in response to government policy and prices. For example, in Acadia parish the 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% in 1985 (Focks et al. 1988b). The values for 1985 were

used in the simulations conducted for the present paper. When untreated, PcSim indicates that 75% of all adults come from rice with ditch and swale and non-rice areas contributing about 12% each. While managing rice acreage for the purposes of mosquito control is obviously not practical, we have included it here to indicate the importance of this parameter in the *Ps. columbiae* problem.

Figure 7 presents simulated seasonal population trends and the frequency of populations exceeding the 2.8 adults/m^2-threshold (insert) as a function of the proportion of land used for first crop rice; it is assumed that second crop rice acreage is one-third that of first crop and that land not used for rice production goes into fallow pasture, soybeans, sorghum, etc. As might be anticipated from the discussion of the population biology of *Ps. columbiae* in the rice agro-ecosystem, PcSim indicates that a decline in rice acreage is accompanied by a corresponding decline in *Ps. columbiae* abundance. PcSim indicates that the elimination of rice culture would
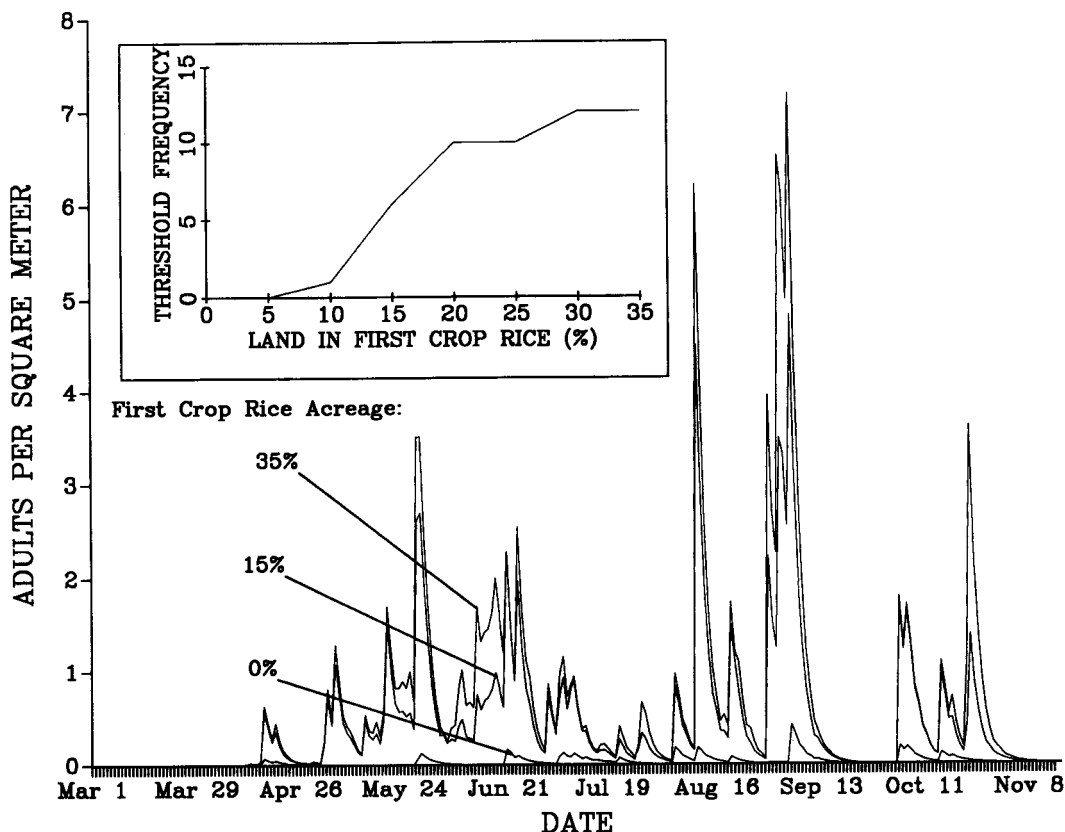
Fig. 7. Seasonal trends of *Psorophora columbiae* adults as a function of rice acreage. Insert presents the frequency of exceeding the 2.8 adults/m²-threshold as a function of the proportion of land used for first crop rice. Second crop acreage is assumed to be one-third that of first crop acreage.

not eradicate *Ps. columbiae* but would likely reduce it to non-pest status. Notice also that planting more than ca. 30% of the total land area to rice does not result in appreciably more mosquitoes as host abundance again becomes the key limiting factor.

Modification of irrigation practices. Certain aspects of rice culture in southwestern Louisiana foster the production of *Ps. columbiae.* Given current varieties of rice, standing water in rice fields is of course unavoidable; it insures that larval development occurs uninterrupted and that oviposition sites are always available. Peak populations associated with reflooding of rice following first crop harvest are also an unavoidable consequence of current practices. However, water management procedures which allow wide swings in water levels during periods of full flood and asynchrony in flooding, harvesting, etc. result in additional *Ps. columbiae* production.

Deeming the synchronization of agricultural events to not be feasible, we investigated the possible role of more accurate water management. Figure 8 presents the water table depths

used in these simulations; only depths in rice fields were changed with depths in the Non-Rice and Ditch/Swale hydrologic areas unaltered. Figure 9 contrasts simulated seasonal trends of adults arising from water management practices representative of current practices in southwestern Louisiana (as described in Focks et al. 1988a) with populations arising from the same system but where water levels were held to exactly the desired nominal depth during full flood in rice (solid line of the bottom panel in Fig. 8). For clarity, only 1 of the 10 representative rice fields used by PcSim is shown.

While maintaining water levels without variation in rice is obviously unrealistic, the results in Fig. 9 suggest the maximum reductions that could be expected. While it is not practical here to describe in any detail the resulting interactions between the modified rice hydrologies and resulting populations from rice and the other hydrologic areas, it is clear that water fluctuation in rice do cause egg hatch and increased adult populations during full flood periods. Contrasting the normal with the modified hydrology,
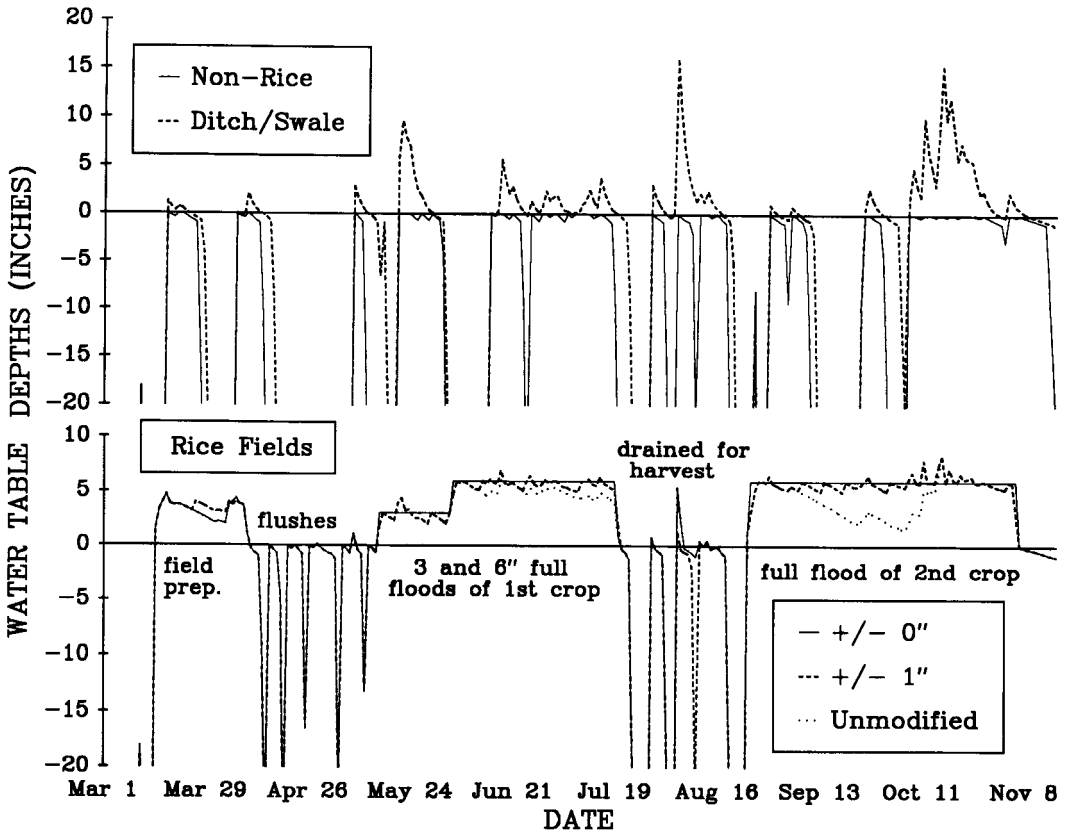
Fig. 8. Water table depths (inches) in the 3 hydrologic areas used by PcSim.

the number of times the 2.8 adults/m²-threshold was exceeded was 17 and 8, and season-long adult densities averaged 0.64 and 0.38/m², respectively. Where 75% of all adults arose from the rice habitat under normal conditions, only 64% of total annual production came from rice when full flood depths were closely maintained to the target depths. The rather significant impact of this modification in rice water management stems from the fact that most *Ps. columbiae* arise from rice in this ecosystem.

Figure 10 presents a similar contrast between adults arising from normal and modified rice water management. Here, water levels were maintained at a more reasonable ±1 inch of nominal levels (dotted vs dashed lines respectively, lower panel, Fig. 8). Frequency of exceeding the spray threshold and average seasonal adult densities were 17 and 9, and 0.64 and 0.54/m², respectively. Under these conditions, the proportion of adults arising from rice declined only slightly from 75 to 73%.

In large measure, the degree of effectiveness suggested here stems from the fact that water levels in second crop rice are typically not as carefully maintained as during first crop (Focks

et al. 1988a) and our proposed modifications differ from current practices most significantly during the second period. We recognize that better water management as a method of mosquito control is probably impractical. These studies do indicate however, that water management does hold some promise.

SOME COMMENTS ON THE POSSIBILITY OF BIOCONTROL

The life-history strategy of *Ps. columbiae* argues rather strongly against the possibility of successful biological control via the one-time introduction of exotic species or the augmentation of indigenous or imported ones. Historically, good candidates for biocontrol have been insects living in essentially permanent and stable environments. Debach (1974), in his book on biological control, lists 15 examples of successful biological control. In each case, the pest inhabited stable environments such as citrus, walnut, shade, or olive trees, orchards, tea plantations, or range grasses. The stability of such environments allowed the continual interaction of pest and biological agent. To quote Service
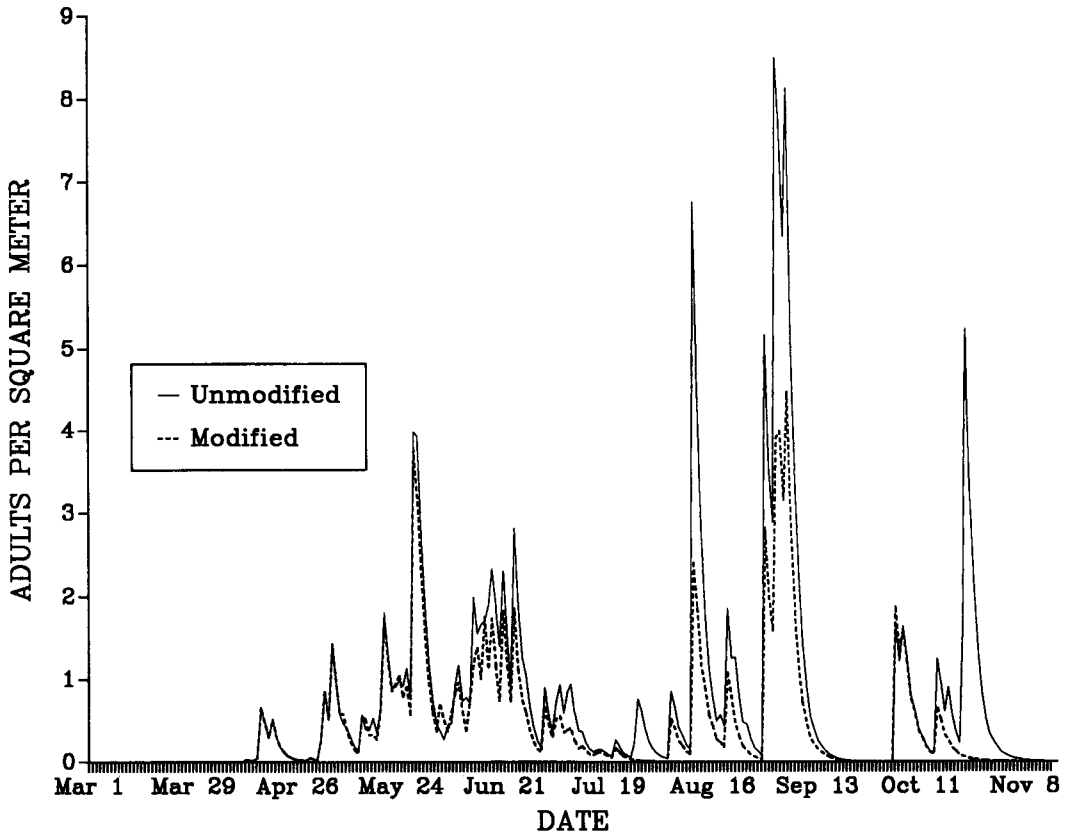
Fig. 9. Comparison of the seasonal trends of *Psorophora columbiae* adults in response to modified irrigation practices (full floods during first and second crop held to exactly the nominal values presented in Focks et al. 1988a) with the standard, reference population.

(1985), "Less success has been achieved in less stable situations, for example, against pests of annual crops and *mosquito larvae in temporary water collections, habitats which are subject to ecological catastrophes such as destruction or desiccation*" (emphasis added).

An additional problem regarding the feasibility of biocontrol of *Ps. columbiae* stems from a lack of parasitoids attacking mosquitoes (Service 1985). Again, successful examples of biological control most commonly have involved parasitoids as they establish tight obligate relationships to their host via high searching efficiencies. The result is the ability to depress host populations to extremely low levels.

An important element of the life-history strategy of an r-strategist like *Ps. columbiae* is its ability to colonize ephemeral habitats prior to their colonization with predators. And while predators are not expected to therefore play a significant role in their more normal habitat, e.g., the non-rice and ditch/swale habitats of the rice agroecosystem, they are significant mortality sources in the less transient rice field (see

Focks et al. 1988a for references). Achieving greater levels of control in rice via predators is a significant challenge in that most if not all predators in this system are polyphagous with corresponding low searching abilities. When mosquito densities are low, the predator complex tends to focus efforts on other sources of food. To quote Service (1985) again, "Low searching efficiency will always tend to occasion high pest-population equilibrium levels". This is certainly the case with *Ps. columbiae*; even though predators are estimated to account for some 80% of all larval losses in rice (Andis and Meek 1985), this species remains a pest.

One final point, assuming there are some good biocontrol candidates, given the ephemeral nature of the habitat, almost certainly mass reintroductions or augmentations would be required as the habitat either regularly dries out (most swale and non-rice habitats) or is treated with toxicants (rice). If the history of reintroduction/augmentation efforts provides any guidance, the outlook for regulating *Ps. columbiae* by this means is probably also, poor at best.
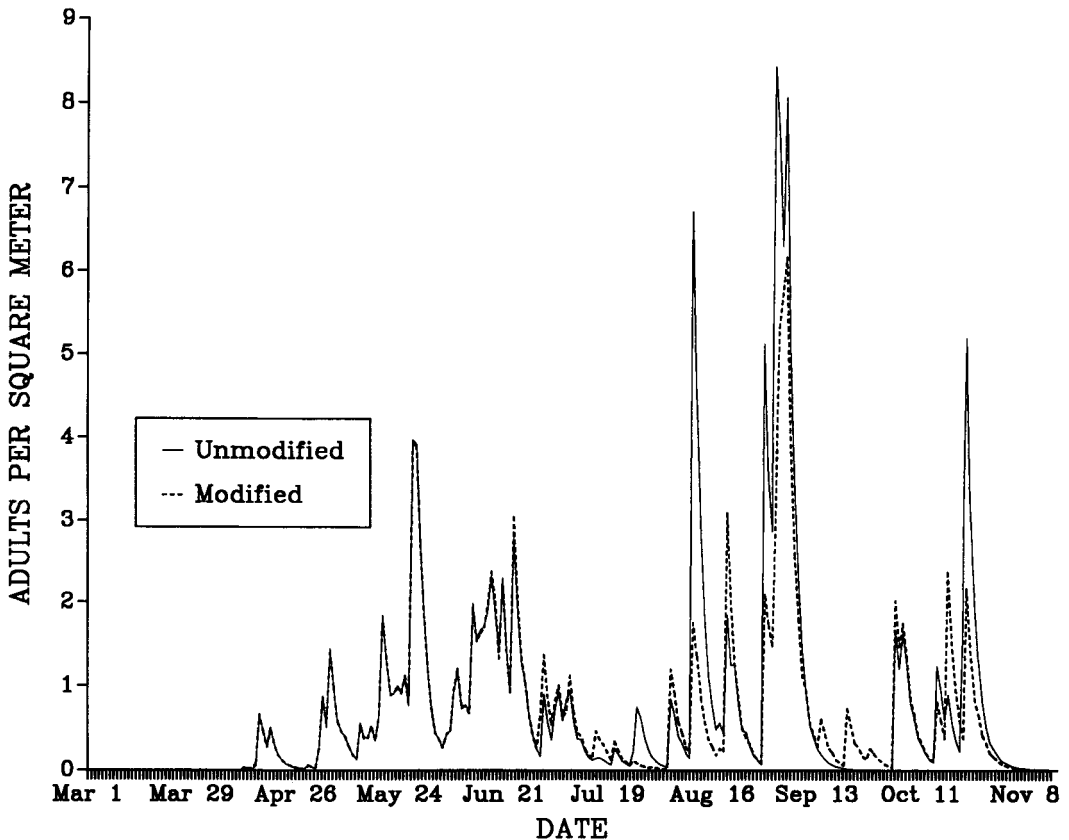
Fig. 10. Comparison of the seasonal trends of *Psorophora columbiae* adults in response to modified irrigation practices with the standard, reference populations. Water levels were held to ±1 inch of nominal levels.

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