TriDyn—A simulation model of the dynamics of *Culex tritaeniorhynchus* populations

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Abstract: In this study a simulation model of the population dynamics of *Culex tritaeniorhynchus* (TriDyn) was developed using the dynamic life table approach. The model took account of the density dependent effects on larval mortalities. A density independent factor reflecting the seasonal variation of survival rates of immatures and females as well as fecundity of females is described using a sinusoid function. The simulation demonstrated the significant role of the density dependent effect in the dynamics of *Culex tritaeniorhynchus* populations, suggesting that the bimodal and fluctuating population dynamics observed in light trap samples in Shanghai may have resulted from an overcompensation of density dependent processes.

INTRODUCTION

Naturally occurring mosquito populations are invariably embedded within a matrix of nonlinear interactions with other populations and environmental variables. To deal with this complicated system and elucidate processes governing dynamics of mosquito populations, computer modelling is becoming increasingly useful (Focks *et al.*, 1988; Haile and Weidhaas, 1977; Scott *et al.*, 1983). Merits of computer models are: 1) summarizing current knowledge of the target mosquito; 2) highlighting areas where additional information is required; 3) testing hypotheses experimentally on a computer; and 4) providing aids for optimizing mosquito management programs.

Culex tritaeniorhynchus is the primary vector of the Japanese encephalitis virus in

some Asian countries. In addition to transmitting the disease, it also poses severe pest problems in some areas. The larvae breed mainly in large aquatic environments, such as rice fields, ponds and ditches. The generation of summer populations is generally overlapped. Research in the past concentrated on various aspects of the life cycle, but little attempt was made to show how the results related to population dynamics. A mathematical model may shed light on population processes and rationalize the optimization of control programmes. As the first step towards this end, a simulation model of the population dynamics of *Cx. tritaeniorhynchus* (TriDyn) has been developed and tested against a field observation.

MODEL DEVELOPMENT

The life cycle of *Cx. tritaeniorhynchus* is

Fig. 1 The model frame of life cycle of *Culex tritaeniorhynchus*.

○, daily age class; ×, variable development times dependent on temperature accumulation.

classified into seven stages, *i.e.* eggs, larvae (including all larval instars), pupae, nulliparous, first, second, and older parous females. Within each stage individuals are divided into daily age cohorts according to their development (Fig. 1). The population processes are simulated by updating individuals in each age and stage on a daily basis.

The simulation was conducted by assuming a given area with maximal water-logged areas of 50,000 m², and neither immigration nor emigration was considered in the model. The initial population size, density independent and density dependent factors were assumed on the basis of literature review and actual simulation results.

1. *Temperature dependent development rates and oviposition cycle.* The thresholds and thermal constants for immature development of *Cx. tritaeniorhynchus* were observed

in the comprehensive study by Mogi (1978), and used in TriDyn. The thermal constants for egg, larva and pupa are 25, 125 and 99 degree days, respectively.

In summer the oviposition cycle of *Cx. tritaeniorhynchus* is 2–3 days (Buei *et al.*, 1980; Gu, 1992). Newly emerging females have to mature and get inseminated prior to the activity of host finding, so the thermal constant of nulliparous and parous females is estimated at 70 and 50 degree days, respectively, assuming the threshold for reproductive activity to be 10°C.

2. *Density independent processes.* The seasonal changes of weather and rice field conditions have substantial impact on mosquito populations. In general, air temperature is highest in July and August when flooded lands are also largest and most suitable for *Cx. tritaeniorhynchus* breeding and

Fig. 2 The seasonal density independent factor during the simulation period.

reproduction (Mogi, 1984). In spring and autumn the physical environment becomes unfavorable for mosquito development and survival as a consequence of a combination of factors such as low temperature and the limitation of larval breeding habitats. In order to reflect the seasonal variation of the population parameters and water-logged areas, a density independent factor at day t ($DI(t)$) is described using a sinusoid function (Fig. 2):

$$DI(t) = \sin[\pi\{t + 0.5(365 - N)/365\}],$$

where N = total simulation days.

The daily survival rates of egg, larva, pupa, female individuals and adult fecundity as well as water-logged areas are multiplied by $DI(t)$ to adjust the seasonal variation.

3. *Density dependent larval mortality.* Although *Cx. tritaeniorhynchus* breeds in large habitats, they usually suffer from under-feeding, and in some cases even space competition in these places (Chubachi, 1979; Mogi, 1978). By using the conversion coefficient to estimate absolute larval density from dipper counts of *Cx. tritaeniorhynchus* (Gu *et al.*, 1992), absolute larval densities in rice fields in Yangzhou, Jiangsu Province were generally below 1,000/m² and exceeded this threshold only in July and August (Gu and Lu, 1989). It is reasonable to assume that density regulation occurs when larval densities peak. Therefore, a survival reduction rate by density dependent factors ($DD(t)$) was designated to be 1.0 (no reduction) at low density (<1,000/m²) and 0.1 at high

Fig. 3 The relationship of larval density dependent factor to larval density.

density (>5,000/m²) (Fig. 3). If larval density exceeds 1,000/m², the density dependent factor ($DD(t)$) will have a regulat-ing effect on larval survival rates.

4. *Population parameters and initial pop-ulation size.* The maximum values of popu-lation parameters were assumed as follows so as to make the values of these parameters fall into the ranges observed in field studies after adjustment for the density dependent and independent effects: daily survival rates of immatures, nulliparous and parous females are 0.95, 0.90 and 0.90, respectively, and fecundity is 250 per oviposition per female. Sex ratio is 0.52 in favour of females. Circumstantial evidences indicates that a portion of the population has difficulty in getting a reproductively competent blood meal. For example, the parity rate of field populations is often very low (Edman, 1991). Therefore, the successful blood feeding rate of a newly emerging cohort was assumed to be 0.50.

The overwintered adults started host search in early April, and reached a high peak in the middle of that month, then gradually declined due to death (Xue *et al.*, 1991). Figure 4 describes the initial population size in TriDyn.

It is assumed that females newly emerging after mid-September are gonoinactive and enter diapause.

5. *Sample survey for model validation.* To monitor the dynamics of *Cx. tritaeniorhynchus* populations, light traps were operated in a dairy of Jiangwan (117°30'E, 31°19'N), northeast of Shanghai, from June 20 to October 20, 1991. The dairy was

Fig. 4 Numbers of reproductively active females after overwintering.

surrounded by a variety of aquatic environment, including ponds, ditches and rice fields, providing ample larval breeding habitats and blood sources. Three light traps were hung under trees (1.8 m above the ground). Trapping was started within 10 min after sunset and lasted for 1 hr. The captured mosquitoes were brought back to the laboratory for species identification. Samples were taken every 4–5 days, and weekly average densities of *Cx. tritaeniorhynchus* were calculated. The meteorological data were obtained from a nearby weather station.

To calculate generation growth rates and generation time an option is devised which enables the development of each generation to be traced separately. Generation growth rate is defined as the ratio of total newly emerging females of two successive generations, and generation time as the period between the first day of the emergence of females of two successive generations.

6. *Model inputs and outputs.* TriDyn is temperature driving, requiring inputs of daily temperature profile and the values of population parameters described above. It can simulate daily total numbers and new recruits of each stage and display weekly means of females simulated and observed light trap catches which have been scaled to the former.

The model, programmed with Turbo-Basic, can be run on any IBM PC/AT or any compatible machines with EGA and EGA monitor. A free copy of the program listing can be obtained from the author.

RESULTS

The weekly means of light trap samples and climate variables in Jiangwan are given in Table 1. The dynamic pattern of *Cx. tritaeniorhynchus* in 1991 in Shanghai was bimodal, with a higher peak occurring in early July and the other in early August. The weekly mean temperature and the number of hot days of concurrent and preceding 2–3 weeks were significantly correlated with light trap catches ($n=17$, $p<0.05$), but other meteorological variables showed no association with trap catches (Table 2).

In general, predicted results of TriDyn were in line with those observed, although there were some discrepancies (Fig. 5). Females of the first generation started to appear in the middle of May. From that time population densities built up quickly and peaked in middle July, then the abundance level fluctuated due to density regulation, but remained at a high level until mid-September.

Under the climate conditions in Shanghai, the model population could complete as many as ten generations per year (Table 3). The first generation suffered substantial deaths as a consequence of low development and survival rates. As mentioned earlier physical environment became favorable to *Cx. tritaeniorhynchus* from June on; therefore, the small population of the first generation underwent exponential growth until mid-July. After that time population growth slowed down and eventually declined. The diapausing females in late autumn were about 9 times more than that of the initial populations; the total mortality of overwintered females was calculated as 89%.

Simulation was also run under various assumptions to obtain insight into the population dynamics of *Cx. tritaeniorhynchus*, especially to clarify the significance of density regulation. When the density dependent factor was excluded from the model, the predicted abundance of newly emerged females constantly increased and peaked in early September. This pattern is obviously not in

Table 1 Weekly means of light-trap captures of *Culex tritaeniorhynchus* and meteorological variables in Jiangwan, Shanghai in 1991.

Date	Temperature (°C)	Humidity (%)	Precipitation (mm)	Rain days	Hot days (>34°C)	Mean No. capture
April 1	13.1	75	4.2	1	0	—
8	15.3	82	6.7	2	0	—
15	14.8	72	4.5	2	0	—
22	15.7	76	12.2	3	0	—
29	16.4	81	8.4	2	0	—
May 6	16.5	78	5.7	3	0	—
13	17.1	75	14.7	3	0	—
20	22.0	72	12.6	2	0	—
27	24.2	81	8.6	3	1	—
June 3	20.9	81	6.3	2	1	—
10	23.6	84	72.6	5	0	—
17	24.2	89	210.1	6	0	—
24	22.1	81	62.5	3	0	153
July 1	27.6	72	30.3	1	2	168
8	25.4	88	149.4	6	0	150
15	27.5	83	47.6	3	2	1,211
22	30.5	76	0.2	1	4	435
29	30.5	77	12.8	2	4	249
Aug. 5	29.3	79	10.5	4	2	379
12	25.0	82	231.5	4	0	698
19	27.4	80	0	0	0	198
26	27.8	77	1.7	1	0	135
Sept. 2	26.8	77	0.3	1	0	37
9	27.0	79	129.2	4	0	46
16	24.0	77	30.5	2	0	22
23	22.2	75	1.6	2	0	15
30	21.0	83	21.7	4	0	3
Oct. 7	20.8	79	40.7	1	0	3
14	19.4	75	0.2	1	0	2

Table 2 Correlation coefficients between light trap catches and climate variables of concurrent and preceding weeks.

Week lag	Temperature	Humidity	Precipitation	Rain day	Hot day
0	0.77**	0.21	0.27	0.17	0.51*
1	0.66**	0.30	0.25	0.28	0.47*
2	0.58*	0.12	0.23	0.13	0.58*
3	0.18	0.26	0.01	0.12	0.50*
4	-0.15	0.46	0.22	0.36	0.31
5	-0.39	0.35	0.16	0.43	0.12

* $p < 0.05$; ** $p < 0.01$ ($n=17$).

Fig. 5 Observed and predicted patterns of *Culex tritaeniorhynchus*.

A: predicted by TriDyn; B: predicted by the model without density dependent factor;
C: observed results in Jiangwan, Shanghai which had been scaled to series A.

Table 3 Total emerging females of each generation predicted by TriDyn.

Generation No.	No. emerging	Increase rate	First occurring date	Generation time (day)
Initial	19,505	1.00	Apr. 1	—
1	330	0.02	May 16	46
2	4,284	12.98	Jun. 2	17
3	20,039	4.68	Jun. 17	15
4	9,189,383	458.57	Jun. 30	13
5	105,928,440	11.53	Jul. 12	12
6	88,108,046	0.83	Jul. 22	10
7	60,314,936	0.68	Aug. 1	10
8	36,362,640	0.60	Aug. 13	12
9	5,500,565	0.15	Aug. 25	12
10	181,053	0.03	Sept. 6	12

accordance with the natural population dynamics (Fig. 5).

DISCUSSION

Temperature affects light trap catches in two ways. Under favorable temperature ranges, firstly, with the increase of temperature the total survival rates of mosquitoes markedly increase as a consequence of shortening the generation time, and the absolute density of mosquitoes in the attracting range

of a light trap will be high; secondly, blood-feeding flight will become more active under higher temperature. Therefore, it is reasonable to find a significant correlation between light trap catches and weekly means of temperature as well as the number of hot days. But the temperature pattern was roughly monomodal and peaked in late July and early August (Table 1), whereas population densities of *Cx. tritaeniorhynchus* peaked earlier than the temperature, indicating that the population dynamics of *Cx. tritaenio-*

rhynchus could not be explained solely by the temperature pattern.

The role of density regulation in mosquito population dynamics remains under debate. Density dependent processes resist changes in population size, whereas the object of the control programme is to reduce population size. Clearly these two processes interact with each other (Service, 1985). Consequently, an understanding of the type and degree of density dependent processes operating on the populations of *Cx. tritaeniorhynchus* is highly relevant to the establishment of control strategies.

The density effects in *Cx. tritaeniorhynchus* have been documented (Chubachi, 1979; Mogi, 1978; Siddiqui *et al.*, 1976), although investigation is hard due to complicated interactions and fluctuations of population parameters and climate variables. The most meaningful insight gained from the simulation is the significant role of population regulation in dynamics of *Cx. tritaeniorhynchus* populations. Despite incorporation into the model of the seasonal variations of population parameters, the population trend simulated was approximated to the observed parameters only after incorporating the density dependent factor. This suggested that the density dependent process has a primary role in the formation of the fluctuating population pattern of *Cx. tritaeniorhynchus*. Simulation experiments also suggested that the fluctuating dynamics resulted from an overcompensation of the density dependent process.

The model showed that the first generation (occurring in April and May) declined markedly compared with overwinter populations (Table 3), indicating that control efforts directed towards this generation may have substantial impact on summer population densities.

Although the behaviour of TriDyn model roughly approximated the field observations, some differences were obvious between them; population densities of light trap sampling peaked abruptly in early July and declined rapidly after August, whereas simulating populations changed somewhat gradually.

The reasons may be as follows. Firstly, as light trap sampling is subject to bias, three light traps may be too few to obtain representative estimations; secondly, the seasonal changes of physical parameters in nature may be abrupt, whereas the seasonal variation of these parameters in TriDyn was described using a sinusoid function which changes gradually.

Effective computer analysis will depend upon the availability of sufficient biological data to make simulations realistic, as well as upon the development of simulation methods that effectively use existing biological data. So far as our current knowledge of the population dynamics of *Cx. tritaeniorhynchus* is concerned, refinement is needed to allow full model validation. Areas of additional research include the relationship between host feeding rates and mosquito densities; the exact forms of the seasonal changes of mortality and fecundity; and the association between flooded coverages and larval densities. With appropriate validation and improvements, TriDyn can facilitate the evaluation and optimization of current proposed IPM strategies for *Cx. tritaeniorhynchus*.

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