

Dispersal of *Culex tritaeniorhynchus* larvae (Diptera, Culicidae) by Water Currents in Rice Fields

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Abstract: Influence of water currents on the dispersal of *Culex tritaeniorhynchus* larvae was studied in a terraced rice field area common in the Nagasaki district, Japan. In rice fields under normal water regulation, water was stagnant except a route connecting the inlet and the outlet. However, emigration rates of *tritaeniorhynchus* larvae from these rice fields were sometimes very high, the maximum estimate being 0.3596 per day. This strongly suggests the possible destructive effect of heavy and/or successive rains on *tritaeniorhynchus* populations in rice fields, especially in terraced ones. An observation to support this was presented. Various aspects of the effect of water currents on mosquitoes in rice fields were discussed in relation to population dynamics and control. Also, significance of larval dispersal was examined in relation to various types of breeding habitats of mosquitoes.

Generally speaking, running-water is unfavourable for the breeding of culicine mosquitoes. Slow-running water such as edges of rivers or ditches is a main breeding source of some anopheline mosquitoes including important vectors of human malaria, but this type of habitats is rather secondary or exceptional in culicine mosquitoes. In Japanese rice fields where artificial irrigation is done, density of *Culex tritaeniorhynchus* larvae is high usually at the stagnant part. However, the effect of water currents has hardly been studied on mosquitoes in rice fields. This study was done to know the dispersal rate of *tritaeniorhynchus* larvae by water currents in rice fields.

PLACE AND METHODS

The study was done in a rice field area in a valley in the suburbs of Nagasaki City. In this area, most rice fields are developed in a terraced manner as usual in the Nagasaki district. For further description of the area, see Mogi (1978b). Water, which is introduced from irrigation ditches, runs from upper rice fields to lower ones mainly

via tiny falls, two examples of which are shown in Fig. 1. Plain maps of rice fields and sluices selected for this study are presented in Fig. 2. The study was done in early-middle July of 1973, when rice plants were about 30 cm or less in height and duck weeds were very small in number.

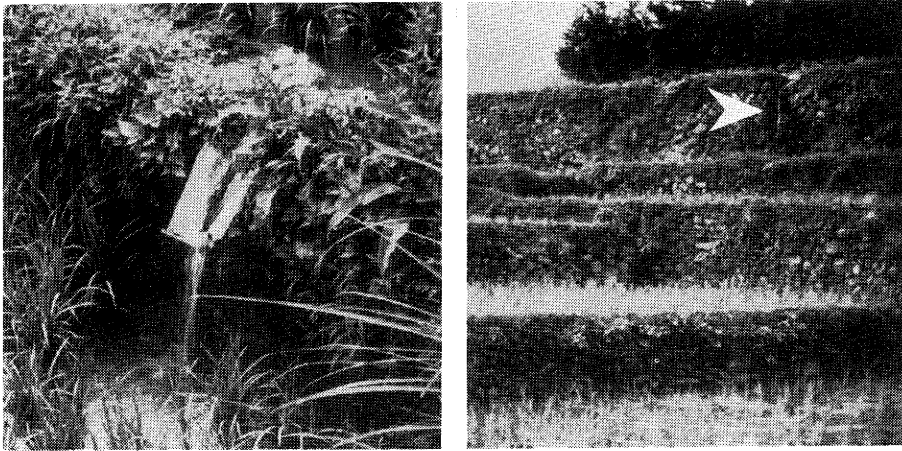


Fig. 1. Water flow at sluices in the terraced rice field area.

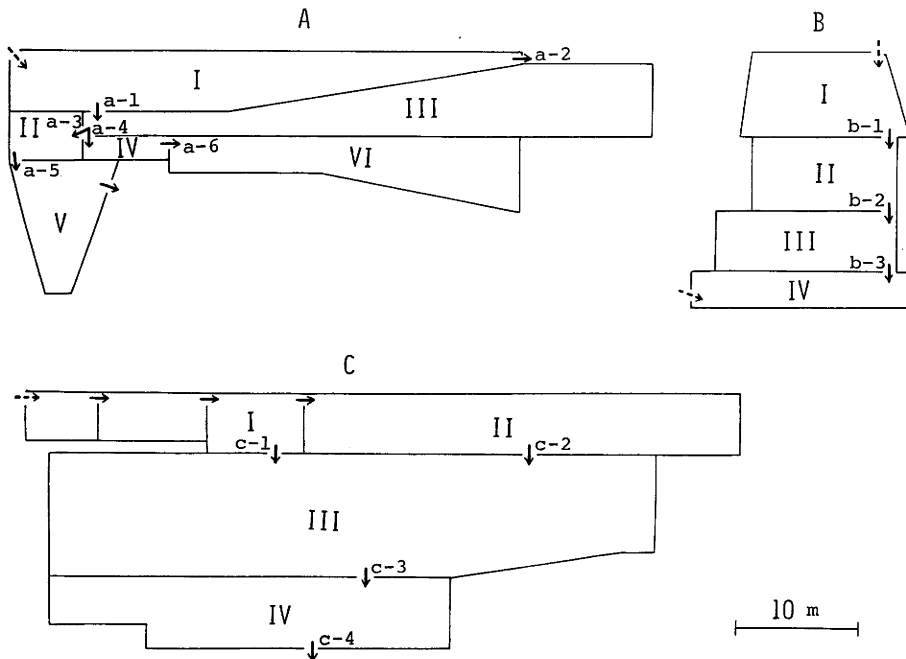


Fig. 2. Plain maps showing the arrangement of rice fields and sluices. Arrows indicate the direction of water currents. Broken arrow : Inflow from irrigation ditches.

Field procedures were as follows :

- (1) Mosquito larvae (pupae inclusive) were dipped at each rice field, and the specimens were preserved in 3 % formalin solution for identification.
- (2) 50 liters of water were taken at each sluice by receiving water in a bucket with scales, and the time required for accumulation of 50 liters of water was recorded. The water was filtered and insoluble contents were preserved in 3 % formalin for the later examination.
- (3) Speed of water currents was examined at various parts of each rice field by observing the movement of paper disks (5 mm in diameter) on the water surface.
- (4) The area of each rice field was measured, and the water depth and the rate of area with water were recorded.

From values thus obtained, the following parameters were derived :

- (A) Mean number of larvae (pupae inclusive) per dip in each rice field
- (B) Mean number of larvae per m² in each rice field = $A \times 186$ (For this conversion rate, see Wada and Mogi, 1974)
- (C) Total number of larvae in each rice field = $B \times \text{Area} \times \text{Rate with water}$
- (D) Amount of water (liter) in each rice field = $\text{Water depth} \times \text{Area} \times \text{Rate with water}$
- (E) Time (minute) required for 50 liters of water to pass at each sluice
- (F) Water flow (liter) per minute at each sluice = $50/E$. This may be either the inflow (F') or the outflow (F'').
- (G) Theoretical time (minute) required for the displacement of the whole water in each rice field = D/F''
- (H) Number of larvae in 50 liters of water taken at each sluice
- (I) Expected number of larvae passing each sluice per day = $H \times 24 \times 60/E$. Larvae in the inflow are immigrants (I'), and those in the outflow are emigrants (I'').
- (J') Expected number of immigrants into each rice field per day = $\sum I'$
- (J'') Expected number of emigrants from each rice field per day = $\sum I''$
- (K) Immigration rate = J'/C
- (L) Emigration rate = J''/C
- (M) Net change in the population size by dispersal = $J' - J''$
- (N) Net rate of the population change by dispersal = $(J' - J'')/C$

RESULTS

Conditions of water in rice fields studied are summarized in Table 1. When water was flowing from a rice field to another or from a irrigation ditch to a rice field on the same plane, the water flow at the sluice was not measured due to technical difficulty (Rice-fields A-I, B-I, C-I, C-II.) In most rice fields the inflow and the outflow were

roughly equal, which means that the water depth in these rice fields were being kept at a more or less constant level. The different situation was observed for some rice fields, where the inflow was distinctly large than the outflow. In extreme cases, no outflow *via* sluices was recognizable despite a considerable amount of inflow (Rice-fields A-VI, B-IV). These rice fields were under the manipulation by farmers to level up the water just on the study day. The proper management of water is a fundamental requirement for the better growth of rice plants, and it is daily routine of eager and careful farmers to adjust the water level. One rice field (B-IV) was being filled with water after the complete drainage during preceding days.

From Table 1, there can be recognized a point of considerable importance in relation to this study. The inflow and the outflow are generally so large that the whole water in each rice field will throughly be displaced in a short time if the water at every part of the rice field is equally involved in the outflow. The minimum theoretical time for the displacement of the whole water was only 23 minutes calculated for Rice-field A-I. Except rice fields where outflow had been stopped or almost stopped (A-V, A-VI, B-IV), the theoretical time for displacement fell within 6 hours. Are most mosquito larvae in a rice field swept down within several hours when sluices are open? Do mosquito larvae wander from a rice field to another restlessly? This is our problem of great concern.

Table 1. Conditions of rice fields studied

Rice field	Area (m ²)	Rate of area with water	Depth of water (cm)	Amount of water (liter)	Number of inlets	Number of outlets	Inflow per min (liter)	Outflow per min (liter)	Theoretical time for the displacement of water (min)
A- I	162.28	1.0	4	6491	1	2	*	280**	23
II	25.01	1.0	4	1000	1	1	3	5	200
III	177.94	1.0	4	7118	1	1	30	27	263
IV	14.91	1.0	4	746	1	1	27	22	34
V	59.67	1.0	4	2387	1	1	5	very small	very long
VI	109.16	1.0	6	6550	1	0	22	0	—
B- I	64.42	0.8	2	1030	1	1	*	18	57
II	76.88	1.0	3	2306	1	1	18	17	136
III	79.56	1.0	3	2387	1	1	17	15	159
IV	46.59	0.9	2	839	2	0	15+**	0	—
C- I	43.50	1.0	3	1305	1	1	*	38	34
II	179.72	1.0	3	5392	1	1	*	26	207
III	441.94	1.0	3	13258	2	1	67**	57	233
IV	186.65	1.0	3	5599	1	1	57	27	207

* Not determined due to technical difficulty.

** Total at two sluices.

Numbers of mosquito larvae in 50 liters of water taken at each sluice are presented in Table 2. Mosquito larvae were found in 9 samples out of 13. The maximum number of *tritaeniorhynchus* larvae per 50 liters of water was 3, that of *Anopheles sinensis* being 9. There were not collected first instar larvae of *tritaeniorhynchus* and pupae of both species. This is natural since these stages were much smaller in number than other stages in the study fields. Susceptibility to water currents may be different among developmental stages, but this data is insufficient to examine this point. Also, the specific difference in the response to water currents can not be examined at present for the lack of the conversion rate necessary to estimate the absolute density of *sinensis*.

Table 3 shows population parameters calculated from the data presented in Tables 1 and 2. *Culex tritaeniorhynchus* were collected in all the rice fields except B-IV where, as mentioned earlier, water was being reintroduced after complete drainage. It may look strange that no *tritaeniorhynchus* larvae were collected from this rice field by the dipper despite 434 expected immigrants per day. However, this impression is not correct. The whole water in B-IV and the inflow to this field were 839 liters and more than 15 liters per minute, respectively. Thus, the inlet of water to this field was opened probably within 1 hour before the census. This means that the expected larval number at the census time was about 18 in total or 0.39 per m² which is equivalent to 0.0021 per dip. In other words, about 500 dips are required to obtain one larva on an average. Therefore, it is not surprising that no larvae were collected by a limited number of dips.

From dispersal rates obtained, two facts of considerable importance can be seen. Firstly, the general level of emigration rates is much lower than those expected from the theoretical time required for the displacement of the whole water in each rice field.

Table 2. Collection records of mosquito larvae at sluices

Sluice	Time required for 50 liters of water to pass (min)	No. of mosquito larvae in 50 liters of water										Others			
		<i>Culex tritaeniorhynchus</i>					<i>Anopheles sinensis</i>								
		1st	2nd	3rd	4th	Pupa	Total	1st	2nd	3rd	4th		Pupa	Total	
a-1	1.65		1	1			2	2	2					4	
2	0.20						0							0	
3	20.83						0							0	
4	2.08						0							0	
5	9.92			1			1							0	
6	2.23		1				1	5	3	1				9	
b-1	2.82		1	1			2							1*	Chironomidae
2	2.92		1		1		2							2*	Chironomidae
3	3.32		1				1	2						2	
c-1	1.30						0							0	
2	1.90						0							1*	
3	0.88				1		1							0	
4	1.88		3				3				1			1	
Total			0	8	3	2	0	13	9	5	1	1	0	16	

* Instars were not determined.

Emigration rates ranged from zero to 0.3596, the mean being 0.0715. These values may not represent very well the true rate for each rice field owing to a small sample taken once a day or the true mean for the study area owing to a small number of rice fields examined. However, it can safely be said that emigration of most larvae by water currents within a day or less time does not occur when rice fields with a few sluices (usually one inlet and one outlet) are under normal water regulation. This indicates that the assumption for the calculation of theoretical time for the displacement of water was not realistic. Water at every part of each rice field is not equally involved in the outflow. This was evidenced from the distribution of water currents in each rice field, the simplified results being presented in Fig. 3. It is very clear that water runs along a route connecting the inlet and the outlet and that the water near this route alone is involved into the current. At the center of this main current, water moves at the maximum speed of 10 or more cm per second, but the speed slows down rapidly with departure from the center and a large part of the water surface remains stagnant. Therefore, larvae can be protected from being washed away insofar as they stay at this safety zone. Further protection against

Table 3. Dispersal of *Culex tritaeniorhynchus* larvae by water currents in rice fields

Rice field	No. of larvae per dip	No. of larvae per m ²	Total No. of larvae	No. of immigrants per day	Immigration rate per day	No. of emigrants per day	Emigration rate per day	Net change in population size	Net rate of population change
A- I	0.16	29.90	4852	*	—	1745	0.3596	—	—
II	7.67	1426.62	35680	0	0.0000	145	0.0041	-145	-0.0041
III	0.94	174.84	31111	1745	0.0561	0	0.0000	1745	0.0561
IV	1.33	247.38	3688	0	0.0000	645	0.1749	-645	-0.1749
V	13.30	2473.80	147612	145	0.0010	0	0.0000	145	0.0010
VI	1.17	217.62	23755	645	0.0272	0	0.0000	645	0.0272
B- I	0.30	55.80	3395	*	—	1022	0.3010	—	—
II	0.68	126.48	9724	1022	0.1051	987	0.1015	35	0.0036
III	4.16	773.76	61560	987	0.0160	434	0.0071	553	0.0090
IV	0.00	0.00	0	434	—	0	0.0000	434	—
C- I	1.70	316.20	13755	*	—	0	0.0000	—	—
II	0.13	24.18	4346	*	—	0	0.0000	—	—
III	1.30	241.80	106861	0	0.0000	1630	0.0153	-1630	-0.0153
IV	1.76	327.71	61167	1630	0.0266	2294	0.0375	664	0.0109

* Not determined due to technical difficulty.

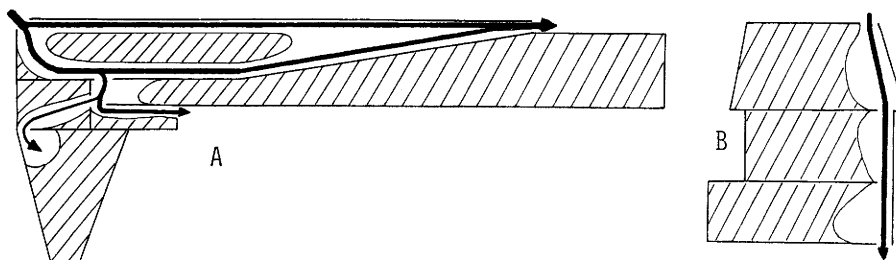


Fig. 3. Water currents in rice fields. Arrows indicate main routes of water currents. Striped area : Stagnant. Open area : Running.

water currents may be given by suitable supporters such as stems of rice plants, and larvae themselves may move upstream in very slow currents. These may be additional factors responsible for actual emigration rates.

The second point seen from Table 3 is that migration rates are often very high even under the condition mentioned above. Emigration rates exceed 0.3 for Rice-fields A-I and B-I, and 0.1 for A-IV and B-II. Immigration rates were generally lower than emigration ones insofar as the present data are concerned, high rates over 0.1 being observed only for Rice-field B-II. Net rates of the population change were small when immigrants and emigrants were nearly equal in number, but very high for some rice fields, the maximum being -0.1749 observed for Rice-field A-IV. The net rates were not calculated for Rice-fields A-I, B-I, C-I and C-II where the number of immigrants was not determined. However, the rates are considered to have been nearly equal to emigration rates at least for Rice-fields A-I and B-I since the water source of these fields was irrigation ditches where water ran fast and mosquito larvae were very scarce. The net rate of -0.3 , for instance, means that the population in this rice field will be decreased to about 0.35 on the third day even without other mortality factors.

The above results lead to the following consideration : if the one-inlet-one-outlet situation is destroyed by heavy and/or long-lasting rains exceeding the control capacity of the irrigation system and water overflows here and there, this multi-slucice situation will force all the water in the rice field to move, which may result in the complete sweeping of immature mosquitoes including eggs, larvae and pupae. One observation to support this possibility is presented in Fig. 4, which shows the difference of water currents and mosquito density between two successive days, 18 and 19 July 1973. This group of rice fields includes B-I~IV where dispersal rates were studied on 18 July 1973. However, larval density per dip is different from that in Table 3. This is due to inclusion in Fig. 4 of culicine species other than *tritaeniorhynchus*. At the night of 18 July, there was a rain of about 30 mm. As a result of the increased water level by this rain, water overflowed at many points. Consequently, the density of culicine mosquitoes was decreased

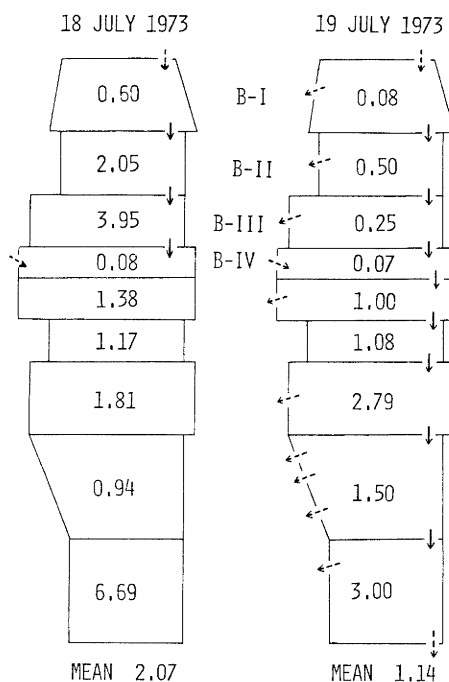


Fig. 4. Changes in distribution and density of mosquito larvae in rice fields caused by water currents after a heavy rain. Numeral: Number of larvae per dip. Solid arrow: Inter-ricefield flow. Broken arrow: Flow from or into irrigation ditches.

in upper rice fields, the reduction rate expressed as (Density on the preceding day—Density on the succeeding day)/Density on the preceding day being 0.9367 at the maximum. In some lower rice fields, the density increased owing probably to immigrants from upper fields, but the mean for all the rice fields was nearly halved from the level on the preceding day. Many larvae are considered to have been swept away from rice fields into irrigation ditches. It is sure that a rain at the night of 18 July strongly influenced the density level and the distribution of larvae in this group of rice fields.

Many factors are expected to influence emigration rates by water currents. One important factor is the relative amount of outflow to the whole water in each rice field as illustrated in Fig. 5. High rates of emigration were observed when the relative amount of outflow is large (theoretical time for the displacement of the whole water is short).

Fig. 6. shows the relation between emigration rates and larval density. High rates of emigration were observed for rice fields with low density. However, this inverse-density-dependency is considered to be apparent. Probably, the true causality which can be seen from Fig. 6 is that larval density is generally low in rice fields where emigration rates are high.

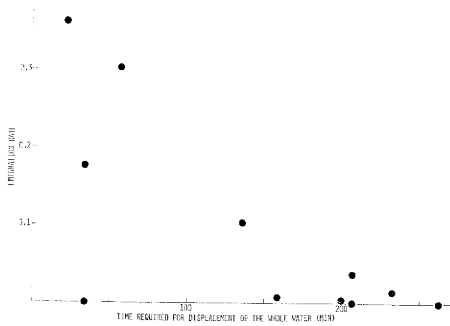


Fig. 5. Relation between outflows and emigration rates.

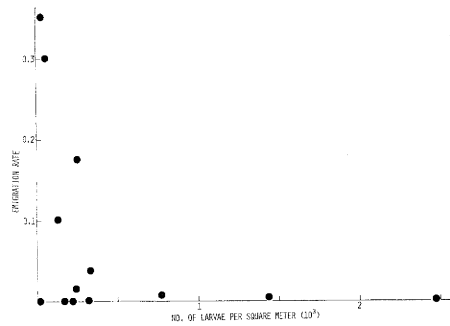


Fig. 6. Relation between larval density and emigration rates.

DISCUSSION

1. Water currents as an important factor influencing the mosquito population in rice fields

It is very clear that the water current is a very important factor influencing the mosquito population in rice fields, especially in small and terraced ones common in the Nagasaki district. The effect of water currents is recognizable most easily when rice fields are flooded by heavy and/or successive rains. A remarkable example demonstrating the destructive effect of heavy rains lasting for several days on the larval population of *tritaeniorhynchus* in the study area was already presented (Mogi, 1978b). This effect may be called "catastrophic" following the term in stream ecology (Minckley, 1964).

On the other hand, it was first demonstrated by this study that dispersal rates of *tritaeniorhynchus* larvae are frequently high also in rice fields under normal water regula-

tion by farmers. This dispersal may correspond to "constant" drift in stream ecology (Waters, 1965). This is not so conspicuous as catastrophic drift but very important to understand the mosquito life in rice fields. How far do mosquito larvae travel from their birth places following water currents in rice fields under normal control? Suppose a series of rice fields through which water flows in due order. If we assume uni-directional dispersal being constant in relation to individuals, rice fields and time, the distribution of larvae among rice fields at the end of the n -th day can be obtained by developing the following binomial formula :

$$(p + r)^n$$

where r is an emigration rate per day and $p=1-r$. Thus, the proportion of larvae in the m -th rice field is given as follows.

$${}^n C_{m-1} \cdot p^{n-m+1} \cdot r^{m-1}$$

The mean emigration rate obtained in this study was 0.0715 per day and the expected duration for the development of *tritaeniorhynchus* larvae in rice fields was 6.69 days at the mean air temperature of 27°C, the average in summer of Nagasaki (Mogi, 1978b). If we substitute 0.1 for r and 7 for n , the distribution of larvae is calculated as follows.

Rice-field 1 (Origin of dispersal)	0.4782969
2	0.3720087
3	0.1240029
4	0.0229635
5	0.0025515
6	0.0001701
7	0.0000063
8	0.0000001

The proportion decreases rapidly in rice fields below the fourth, and more than 0.97 of larvae are expected to pupate in upper three rice fields. However, departure from the assumption may be considerably large when the inlet and the outlet are very close each other. In this case, larvae once involved in water currents would be washed down rapidly and travel a much longer distance than the above expectation. A different probability of dispersal is necessary to be set up for larvae once involved in currents. Therefore, the present assumption may be most appropriate for large rice fields with outlets distant from inlets. In this case, however, a daily dispersal rate of 0.1 may be too high since the value was set up following the one obtained for rice fields including very small ones. If we substitute 0.05 for r , the expected proportion in upper three rice fields increases to 0.9962. Therefore, it may be said that most larvae pupate in three rice fields including the one where they hatched, when large rice fields are under normal water regulation. It is significant that about 0.26 of pupae will occur in the second rice field even when r is 0.05. Evaluation of migration rates is essential when we intend detailed population studies such as the estimation of mortality in respective rice fields.

We once stated that the larval density of *tritaeniorhynchus* in each rice field is

determined by the number of eggs laid there and the survival rate of larvae (Mogi and Wada, 1973). It is evident now that immigration and emigration must be added. Larval density would be highest in rice fields with high density of eggs, high survival rates, high immigration rates and low emigration rates. Water currents influence directly migration rates and also indirectly egg density and survival rates through their effects on the quality of water, since the attractiveness of water to gravid females and the amount of food for larvae are both functions of water quality.

2. *Water currents as a method to control mosquitoes breeding in rice fields*

Surtees (1970), who examined the effect of water currents on mosquito larvae in the laboratory, suggested the possible control of rice field mosquitoes by artificial water currents planned to sweep away the larvae. As stressed by him, the continual loss of larvae may reduce the population significantly even if the disappearance rate per unit time is not very large. For instance, the loss of 0.05 part of larvae per day results in, after 10 days, the loss of larvae equivalent to more than 0.4 part of the initial number even without additional mortality factors. Therefore, introduction of or improvement in the irrigation system can be counted among measures which may be incorporated in the integrated control system against rice field mosquitoes. The reduction in the area of stagnant water through the proper rearrangement of sluices will level down the populations of rice field mosquitoes susceptible to water currents. When a rice field area is newly developed, it is ideal to plan a irrigation system which minimizes the area of stagnant water.

It is better that the specific difference in the response to water currents is studied before the modification of irrigation systems for the control of mosquitoes. According to Mattingly (1969), larvae of *Anopheles minimus*, an important vector of human malaria in Southeast Asia, can resist currents of 0.3 feet per second when they attach to banks. This speed is comparable to the maximum observed in this study (10 cm per second at the center of main currents), and *tritaeniorhynchus* larvae are quite susceptible to this grade of speed. The specific difference is very large in the ability to resist water currents. Therefore, the successful control of one species by artificial water currents may be followed by the increase of other species. To avoid this type of danger, it is most desirable that any control method is introduced after the full evaluation of its effect on the total mosquito fauna as well as on the target species. Also, it must be considered the influence on organisms other than mosquitoes, especially rice plants and rice pests.

3. *Significance of active dispersal of mosquito larvae in relation to their habitats*

Active dispersal due to overcrowding is a fundamental process regulating animal populations. Overcrowding compels animals to disperse through three different ways. They are interference among individuals, conditioning of environment, and exploitation of resources, especially starvation due to food shortage. As for mosquito larvae, interference and starvation has been reported as factors accelerating dispersal. For instance, Nakamura

(1979) observed experimentally that *tritaeniorhynchus* larvae move actively at high density. Also, active movement of starved larvae is familiar to mosquito students who have experience in rearing larvae. An observation for *tritaeniorhynchus* larvae was presented in my preceding paper (1978a). However, little has been discussed on the significance of active dispersal of mosquito larvae in nature.

Significance of active dispersal would be different among different types of larval habitats. Overcrowding with severe food shortage may be very common in small habitats of container types, but emigration from these habitats is practically impossible. Therefore, significance of active dispersal would be very small there, if any. Mattingly (1969) suggested active dispersal of *Tripteroides nepenthicola* from one pitcher to another.

On the other hand, severe starvation due to overcrowding may occur but rarely in large ground pools such as rice fields where larval density per unit volume of water seldom reaches such high levels as frequently encountered in small habitats of container types. Therefore, the absolute amount of food would usually be sufficient if all food were easily accessible for mosquito larvae. However, food density is often not fully high in these habitats as exemplified for *tritaeniorhynchus* in rice fields (Mogi, 1978b). This may be called "relative shortage of food" following Andrewartha and Birch (1954). In this condition, active dispersal may help larvae to follow the micro-difference in the food concentration within a pool. Ikemoto and Sakaki (1979), who studied the distribution of *Anopheles sinensis* larvae in rice fields, found a positive correlation between the larval density and the $\text{NH}_4\text{-N}$ concentration within a rice field and attributed this to intra-ricefield migration of the larvae.

Density effects and food levels have scarcely been studied for mosquito larvae preferably inhabiting in running water, but active dispersal might be most significant in these species in view of the presumed low density of food and the open structure of their habitat. Also, passive dispersal due to heavy and/or long-lasting rains would be most destructive in this type of habitats. Therefore, the role of larval dispersal in the population dynamics of running water breeders is a fascinating problem. It is very interesting whether or not the hypothesis of "colonization cycle" can be applied to mosquitoes breeding in running water. This theory, which was presented for insects with larval stages as the benthos of streams and evidenced for some species, includes downstream drift of immature stages and upstream flight of adults prior to oviposition (Müller, 1954).

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水田の水流によるコガタアカイエカ幼虫の分散
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水田内の水流によるコガタアカイエカ幼虫の分散量を知るために、長崎に多い段丘水田地帯で調査をした。正常に水管理されている水田では、通常、取り入れ口から出口に向う細い流れが生じるだけで、そこから離れると水の動きはなくなった。しかし、そのような水田でも、コガタアカイエカ幼虫の流出量は非常に高い場合があり、1日あたり推定流出量の最大値は35.96%であった。従って、豪雨や長雨によって水田が氾濫した場合には、コガタアカイエカ幼虫個体群は懐滅的な影響を受けると予想される。この推測を裏づける一観察例を紹介した。これらの結果にもとづき、水田に発生する蚊に対する水流の影響を個体群動態や防除法と関連づけて論じた。また蚊幼虫の分散の意義についても、発生場所のタイプごとに考察した。

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