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Population Studies on Mosquitoes in the Rice Field Area of Nagasaki, Japan, Especially on *Culex tritaeniorhynchus*

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Abstract : Ecological studies were done on mosquitoes breeding in rice fields. Both adults and larvae were collected with a regular interval of one week in a rice field area of Nagasaki, Japan. There were collected 18 species, among which dominant were *Anopheles sinensis* and *Culex tritaeniorhynchus*. The latter is a principal vector of Japanese encephalitis (JE) virus in our country, therefore its population was studied in detail. From the results of regular censuses, other experiments and various observations, the following points were indicated. (1) Active reproduction occurs almost exclusively in July when both oviposition and pupation rates are raised greatly by extension of suitable breeding places following transplanting of rice plants. (2) Major factors to influence reproduction of the species are temperature, precipitation, water management of rice fields, availability of hosts, chemicals applied to rice fields, and natural enemies, among which the first two are responsible for the yearly change of population size, while the change in the mean population level is attributable to other four factors which are controlled or influenced by man. (3) A combination of high temperature and small precipitation in summer is considered to be best for reproduction of the species. (4) However, all the above factors are density-independent in their action, the population being regulated by density effects due to overcrowding of larvae (see Section 6.6.19). Based on these results, factors responsible for recent decrease of *tritaeniorhynchus* in Japan was examined, and the primary factor was considered to be the change in the kind of chemicals applied to rice fields, that is, replacement of formerly dominant chemicals with ones being more efficient to *tritaeniorhynchus* and less toxic to natural enemies (see Section 7.4). Lastly, the method to control *tritaeniorhynchus* was discussed. It was clearly shown by simple simulation study that efficiency of chemicals in suppressing the reproduction of the species can greatly be increased by simultaneous application to areas as many as possible (see Section 8.1). Also, it was suggested that extensive use of light traps at animal sheds may be most promising to keep the population of *tritaeniorhynchus* at a low level (see Section 8.2). Epidemiological status of JE in our country is quite different from other mosquito-borne diseases such as malaria or filariasis whose recurrence of a considerable scale is improbable when once the causative parasites are eliminated from Japan. If the population of *tritaeniorhynchus* explodes under a suitable combination of meteorological factors (generally, high temperature plus small precipitation), it immediately will be followed

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by a large recurrence of JE even after very small or no epidemics during a considerably long period of years. The epidemic may even be enlarged owing to the decreased rate of immunized people during the period without large epidemics. Therefore, the preventive system against the epidemic of JE should be maintained and improved as far as *Culex tritaeniorhynchus* and its preferable hosts sensitive to JE virus occur in Japan (see Section 9.1).

1. Introduction

The principal vector of Japanese encephalitis (JE) virus in Japan is *Culex tritaeniorhynchus*, the main breeding place of which is rice fields. Not a few ecological studies were done in Japan and other countries on this species. They revealed various aspects of the species population, but our knowledge is still not enough to control the species by the method reasonable from an ecological point of view. It is needed not merely to suppress the *tritaeniorhynchus* population under the level below which the prevalence of JE does not occur but to attain it with the least undesirable side effect on both the human health and the biota in the rice field area.

It is not easy, however, to study populations of *tritaeniorhynchus* and other mosquitoes breeding in rice fields, since conditions of rice fields in Japan are highly variable both seasonally and locally insofar as the breeding of mosquitoes is concerned. It is usual that ecological conditions for mosquito breeding are quite different among rice fields lying side by side. Further, mosquitoes breeding in rice fields generally have a very strong ability to fly in the adult stage. These and several other features (overlapping of generations and so on) make the analysis of *tritaeniorhynchus* populations quite difficult both in theoretical and practical aspects. This study could not escape from this limitation. Most results obtained are not conclusive but suggestive, but there included is some new information which may be useful or stimulative for future studies. In the following, there will be presented the main results, based on which, both the factor responsible for recent decrease of *tritaeniorhynchus* in Japan and the method to control the species will be considered, too.

2. Places and Methods

The Nagasaki district is in the westernmost part of Japan. It is a narrow peninsular of complicated form including numerous islands in the East China Sea. Thus, neither rivers nor plains of considerable scales are found there. Rice field areas are developed along streams but generally in a very small scale and are more or less isolated each other. Terraced rice fields of small size are predominant.

A map showing the distribution of rice field areas in the suburbs of Nagasaki City (Fig. 1) may be helpful to visualize the situation mentioned above. Along larger streams near the sea, developed were larger rice field areas, one of which was selected as the station for this study. The majority of other rice field areas were much smaller, and lay scattered at the foot of low hills or between/among them. Most streams which supplied such small rice field areas with water were too small to be properly drawn on the map of this scale.

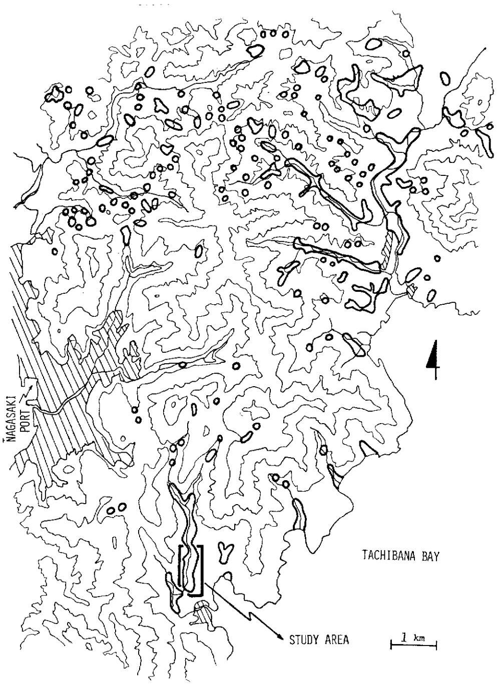

Fig. 1. Distribution of rice fields in the suburbs of Nagasaki City. Thick line : outline of rice field area. Stripes : densely housed area. Contour lines are drawn at intervals of 100 m above the sea level.

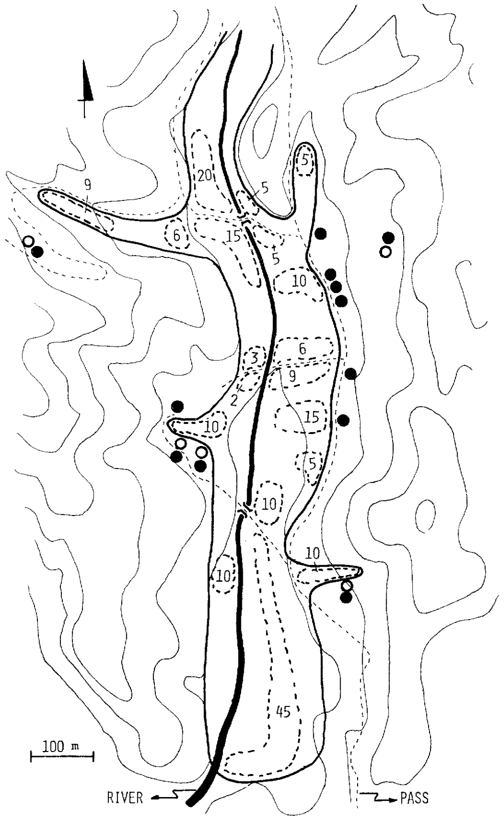

Fig. 2. Study area. Rice fields were developed within the thick line. Rice fields in broken lines were examined for respective numbers. Hollow circle : pigsty. Solid circle : house.

The total area of rice fields in the study station was about 15 ha (Figs. 2 and 5A). The number of included rice fields was about 500, therefore the average area of one rice field was 300 m^2. At the foot of hills surrounding the rice fields, there were farmers' houses and several pigsties. Dogs, cats and hens were found, but they were small in number. There inhabited no wild animals which could be important as hosts of *tritaeniorhynchus*. Judging from knowledge on the feeding preference of the species, pigs were undoubtedly the main blood source in this area during the years when this study was done.

The Nagasaki district locates in the north temperate zone, therefore the seasonal fluctuation of air temperatures is very large (Fig. 3). Ten-day-average air temperatures are lower than 15°C, maybe about 10°C, in late March when overwintered *tritaeniorhynchus* females begin to take blood. Contrarily, those in summer may exceed 28°C. The seasonal distribution of precipitation, which is of fundamental importance to understand the dynamics of mosquito populations, will be mentioned later (see Section 3). Meteorological data are based on Monthly Report of the Japan Meteorological Agency.

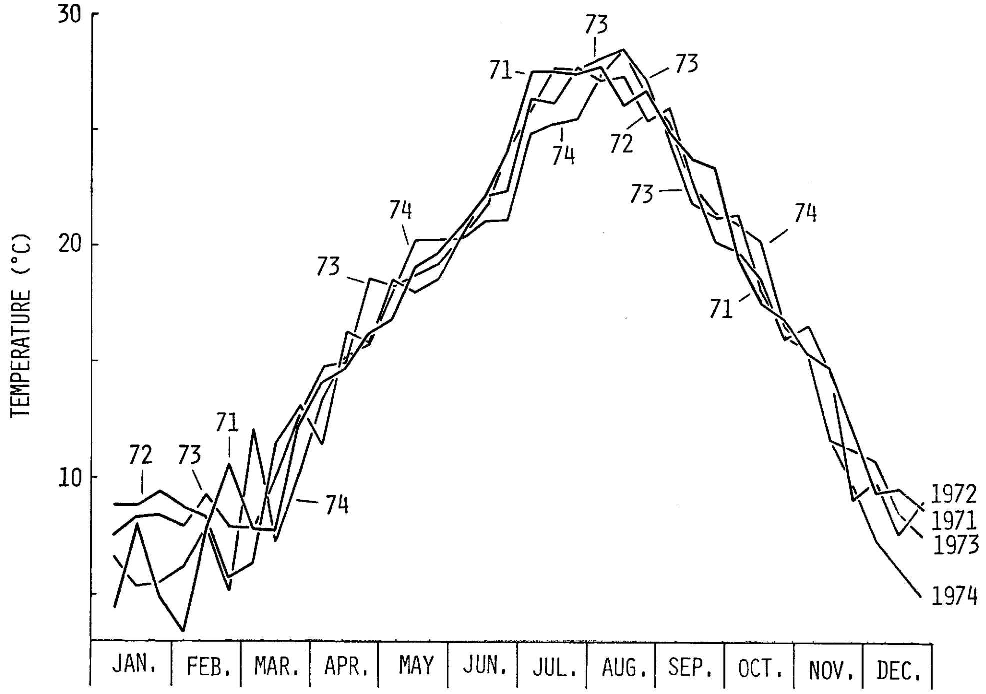

Fig. 3. Ten-day average temperatures at Nagasaki, 1971–1974

To estimate the density of larvae and pupae, 200 fixed rice fields were dipped from April to October at one-week intervals during four years from 1971 to 1974. As was demonstrated already (Wada *et al.*, 1971b), the density of immature *tritaeniorhynchus* in an area can be estimated with the maximum efficiency by increasing the number of rice fields examined and reducing the number of dips per rice field to the minimum (=1). Therefore, only one dip was taken from each rice field, which made it possible to examine as many as 200 rice fields selected from various parts of the study area (Fig. 2).

The dipper was 15 cm in diameter and 3 cm in depth. Contents of each dip were poured into the concentrator, through which all the organisms and other insoluble matter were concentrated in 30 ml of water in a tube with a pinch cock. In principle, this device is similar to concentrators used by various investigators for sampling aquatic stages of mosquitoes (see Service, 1976). By opening the pinch cock, all the contents in the tube were dropped into a plastic jar containing 3 ml of formalin and were preserved for the later examination.

Adult females were collected by a dry ice trap set up in or near the rice field and by an aspirator at two fixed pigsties from March to October at one-week intervals. The dry ice trap was operated for one hour around or after the sunset to cover the evening peak of *tritaeniorhynchus* females attracted to the bait (Mogi *et al.*, 1970). After that, females resting on the inside wall of pigsties or taking blood from pigs were collected by a man for 10 minutes per pigsty. The census of adult populations was done from 1965 to 1974, and a part of the results were published already (Wada *et al.*, 1975 and so on).

Methods of experiments or examinations other than the regular census will be explained with their results. A part of experiments were done in rice fields of the Nagasaki Agriculture and Forest Experiment Station.

For saving the space in tables and figures, larvae of each instar and pupae may be designated as L1, L2, L3, L4 and P.

3. Process of Rice Culture in the Study Area

The process of rice culture in the study area is shown in Fig. 4, taking 1971 as an example. The timing of each work may somewhat be moved yearly or locally but only a little insofar as the years when this study was done.

From November to next May, most rice fields are in fallow with little interference by man. The winter cultivation of other crops is rare in this region. Therefore, rice fields in fallow may be classified into two types. One is wet fields (Fig. 5B) and the other is dry ones (Fig. 5C). The former more or less keep water irrespective of rainfalls and maintain vegetation tolerable to the wet ground, although typical marshy vegetation including perennial plants does not develop owing to repeated summer cultivation of rice plants. Contrarily, the latter keep water only for a short period after heavy rains unless artificial irrigation is done. A dominant plant in dry fields is the milk vetch *Astragulus sinicus* which becomes good manure by being ploughed into the land.

The first work in rice culture is cutting or burning weeds which starts in May. They are followed by ploughing. Irrigation is begun immediately after ploughing in a part of rice fields (Fig. 5D). In late May, a part of ploughed fields are made into nursery beds keeping shallow water (Fig. 5E), and seedlings are grown there until transplanting at the end of June or the beginning of July (Fig. 5F). After transplanting, rice plants become luxuriant day by day, ear in late August (Fig. 5G), ripen in October and are harvested at the end of that month.

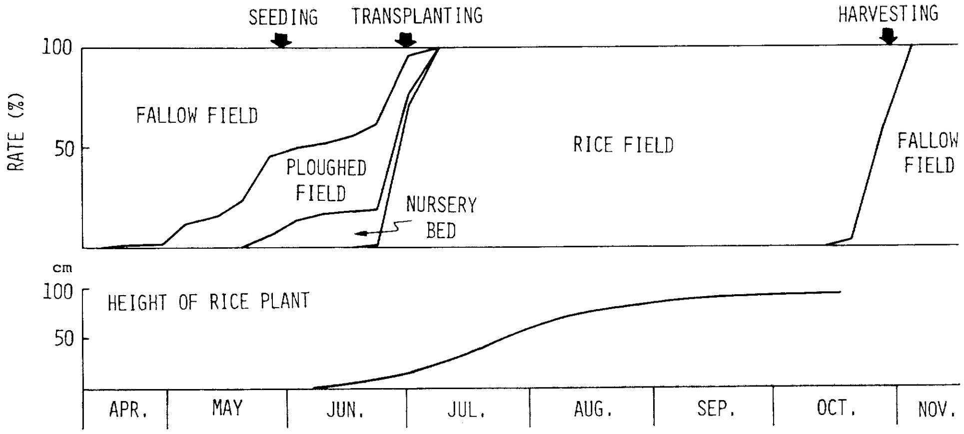

Fig.4. Process of rice culture in the study area (1971)

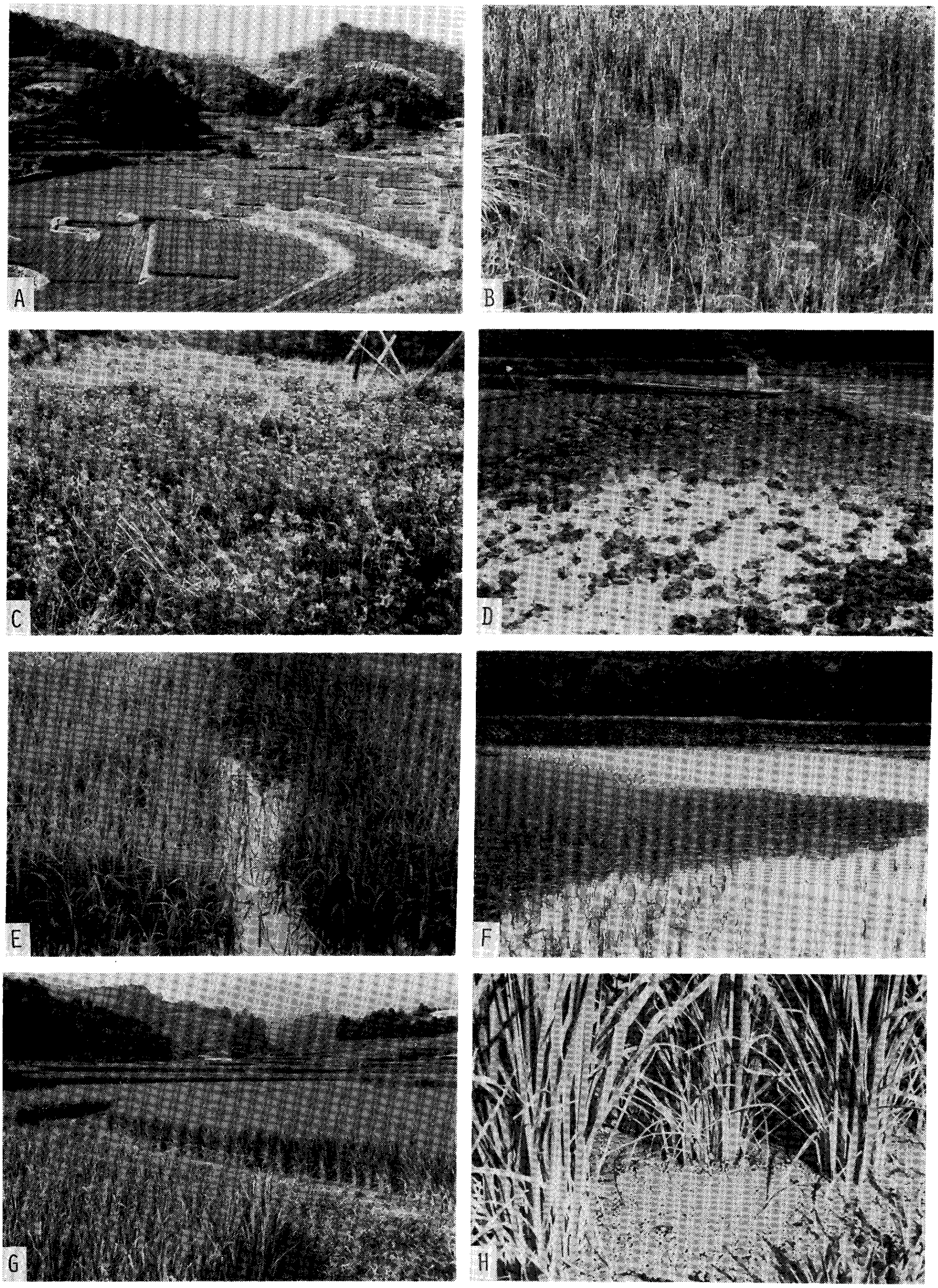

Fig. 5. Rice fields in the study area. (A) Whole view. (B) Wet field in fallow (April–May). (C) Dry field in fallow (April–May). (D) Ploughed field under irrigation (May–June). (E) Nursery bed (June). (F) Rice field just after transplanting (early July), (G) Rice field (middle August). (H) Water surface covered with duck weeds (middle August).

A part of rice fields, however, are not cultivated even in summer, being in fallow throughout the year. Rice fields of this type will be called as "uncultivated rice field" in this paper. They should not be confused with "rice field in fallow" or "fallow field". Both cultivated and uncultivated rice fields are in fallow from late autumn to early summer. When we say "rice field" without special explanations, they mean all the rice fields including fallow, cultivated and uncultivated ones. The rate of uncultivated rice field was negligible in the years before 1970, but increased rapidly since then following the turn in agricultural policies due to the overproduction of rice (Table 1).

Table 1. Numbers (and percentages) of cultivated rice fields and uncultivated ones examined

Year	Cultivated	Uncultivated	Total
1971	187 (93.5)	13 (6.5)	200 (100.0)
1972	180 (90.0)	20 (10.0)	200 (100.0)
1973	159 (79.5)	41 (20.5)	200 (100.0)
1974	165 (82.5)	35 (17.5)	200 (100.0)

The fundamental pattern of water management in cultivated rice fields is as follows: rice fields are filled with water for about one month after transplanting, then irrigation and drainage are repeated with the interval of 5 to 10 days until the constant re-flooding in September, and in October all the fields are drained in advance of the harvest. This is, however, a principle and not necessarily practised by farmers except for the early irrigation and the last drainage.

Observed rates of the water-logged surface area are shown in Fig. 6 with daily precipitation. The rate in uncultivated fields had been expected to change following the seasonal distribution of precipitation, but the actual ones were not necessarily parallel to the latter. Probably the observation of one-week intervals was insufficient to catch without fail the temporary increase of the water-logged area. Also, it may look strange that the rate of water-logged area was lower constantly in uncultivated fields than in cultivated ones even in spring when both types of rice fields are in fallow, but this can be understood in view of the fact that most typical wet fields are cultivated. Before transplanting, the water-logged area in cultivated rice fields fluctuates generally in the same pattern as in uncultivated ones. With transplanting, however, the water-logged area in cultivated fields increased greatly, and the resultant high level was almost maintained throughout the summer season. As mentioned a little earlier, rice fields may be drained, especially in August. However, the operation was done by each farmer independently, therefore no drastic falls in the water-logged area were observed when all the rice fields were totalled. This is seen from Fig. 7 which shows the frequency distribution of water-logged rates in each cultivated field in 1971. In the period shortly after transplanting (early July), most cultivated fields were filled with water completely or nearly completely, the rate less than 0.3 being not found. In the late season, artificial drainage produced another peak in the range less than 0.3, but this peak was small. On the other hand, the water-logged area in uncultivated fields was very small in summer, probably

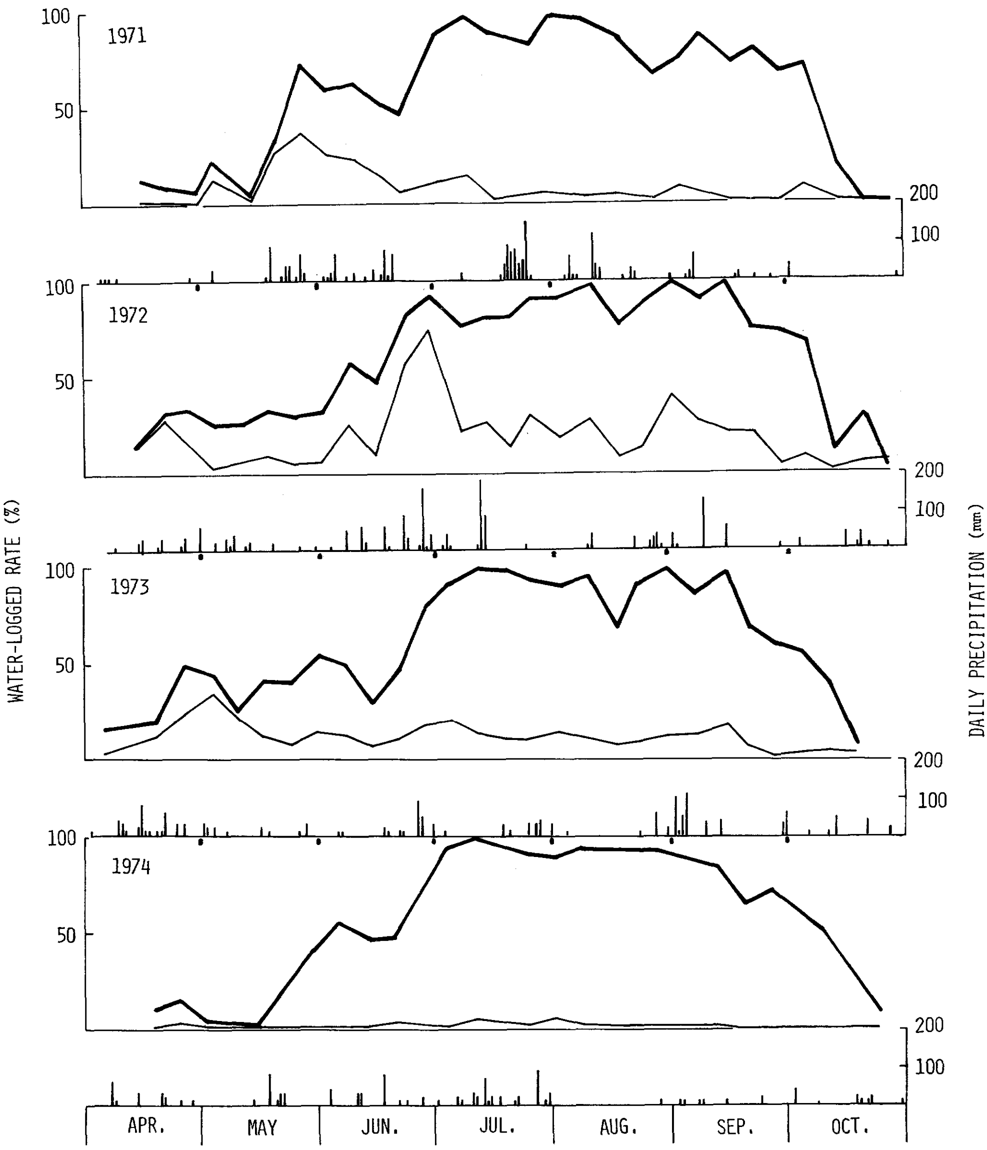

Fig. 6. Water-logged rates in the study area and precipitation at Nagasaki. Thick line : water-logged rate in cultivated fields. Thin line : water-logged rate in uncultivated fields. Vertical bar : daily precipitation.

because of generally small precipitation and large evaporation rates in this season.

Various chemicals are applied to rice fields. The frequency of application varies from year to year and/or from field to field (from farmer to farmer), but the following schedule may be helpful to understand the general tendency in Nagasaki during the years from 1971 to 1974.

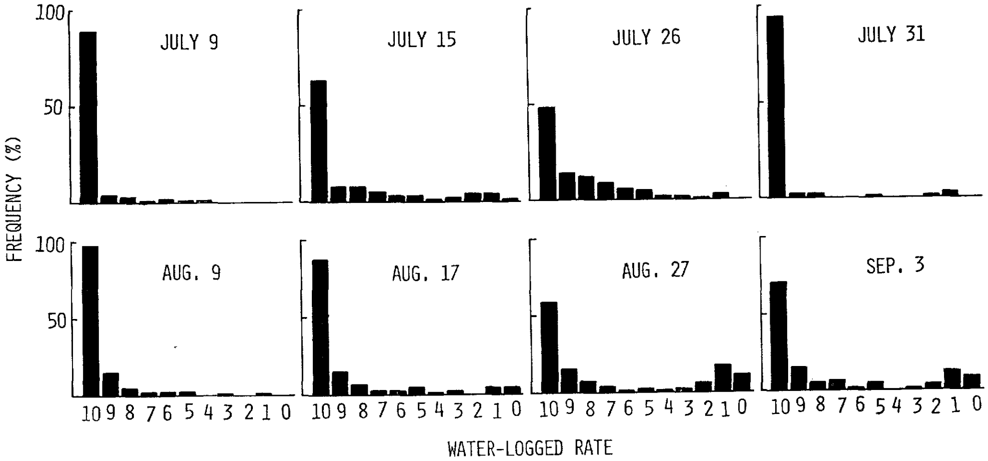

Fig. 7. Frequency distributions of the water-logged rate in cultivated fields (1971). Water-logged rate (%) 1 : 1-10. 2 : 11-20. 3 : 21-30. 4 : 31-40. 5 : 41-50. 6 : 51-60. 7 : 61-70. 8 : 71-80. 9 : 81-90. 10 : 91-100.

- Fertilizers : four times a year
  - first : in May in nursery beds
  - second : in July before transplanting
  - third : in July after transplanting
  - fourth : in August before the earing of rice plants
- Insecticides : five times a year
  - first : for leafhoppers in nursery beds
  - second : in early July for rice stem borers
  - third : in late July for leafhoppers
  - fourth : in August for rice stem borers
  - fifth : in September for leafhoppers
- Fungicides : twice a year
  - first : in August for the prevention of the sheath blight disease
  - second : in September for the prevention of the blast disease
- Herbicides : twice a year
  - first : in July for weeds
  - second : in August for weeds

It is clear that a very large amount of chemicals are thrown into water or dusted on rice plants, although the actual frequency of application may be fewer because of the application of mixtures of two or more chemicals. However, co-operative application was not made in this area, therefore there always existed various rice fields in relation to chemicals.

4. Species of Mosquitoes Collected in This Study

The seasonal distribution of larvae plus pupae dipped from rice fields and the yearly total number of adult females collected by dry ice traps or at pigsties are shown in Tables 2 and 3. Based on these results and other observations, brief notes on the biology of respective species will be given in the below. In total collected were 18 species, of which four were encountered only as larvae and five only as adults. It should be added that they do not represent the complete fauna in this area, since limited kinds of collection methods were used in this study.

Anopheles lindesayi japonicus Yamada: Adult females were collected in spring or autumn by dry ice traps. Larvae were found in a clean ground pool at the foot of a hill but not encountered in rice fields. The feeding habit of the species is quite vague in our country. Omori (1952) observed that caged females readily bite man but he also indicated that the species is seldom attracted to man in the field.

Anopheles hyrcanus group: Besides *Anopheles sinensis* Wiedemann, a very small number of *sineroides* Yamada were collected both as adults and fourth instar larvae. Also, *lesteri* Baisas and Hu may have been included. The occurrence of *sineroides* larvae in rice fields was evidenced by the fourth instar, but separation of *lesteri* larvae from *sinensis* was impossible even in the fourth instar. In the study area, however, both species were much smaller than *sinensis* in number, therefore they can be included in *sinensis* without a significant bias. Practically, young larvae of three species are indistinguishable each other.

Anopheles sinensis is a dominant species not only in this group but also among mosquito species collected in this area. The number of *sinensis* larvae plus pupae was distinctly larger than that of *tritaeniorhynchus* without exception, while adult females of the latter not rarely exceeded the former in number. This interesting phenomenon is not restricted to Nagasaki. Kamimura and Watanabe (1976), who studied rice field mosquitoes in Toyama, central Japan, considered that four factors can be responsible for this phenomenon, but the truth is unknown.

Larvae of *sinensis* were found in rice fields at least from March to November. A considerable number of adult females were not rarely attracted to baits in the earlier or the later season, occasionally even in the midwinter (Wada *et al.*, 1973). Therefore, larvae may occur throughout the winter season in the warm year. Numbers of both adults and larvae decreased in August and increased again in September. Earlier investigators, Koidzumi and Tsuchiji (1925) and Nomura (1943) noticed the similar phenomenon in Taiwan and Japan, respectively. Nomura (his theory was presented collectively in the textboox published in 1947) attributed it to ill effects of high temperatures over 25°C on fecundity with an experimental evidence. High temperatures alone, however, may be insufficient to explain the fact throughly, in view of the geographically wide distribution of the species. It reaches Indonesia in the south, and is said to be a dominant species breeding in open environment in Thailand (Harrison and Scanlon, 1976). As for another possible factor, see Section 6.6.15.2.

Aedes japonicus Theobald: A small number of adult females were collected by dry ice traps and at pigsties, but no larvae were found in rice fields. This is a container breeder, but larvae are found occasionally in ground pools in forest. The feeding habit in natural conditions is not clear.

Aedes nipponicus LaCasse and Yamaguti: Adult females were collected by dry ice traps and at pigsties, but only very rarely. This is a forest species breeding in tree holes, and apparently uncommon in the study area.

Aedes albopictus Skuse: This most common biter in the daytime breeds exclusively in containers of various types. We were bitten by the species frequently when resting in the shade of trees at the foot of hills, but the number of females collected at night by dry ice traps or at pigsties was small.

Aedes vexans nipponii (Theobald): Adult females were attracted to baits from April to October without a regular trend of the seasonal distribution. The number of this species ranks next to *tritaeniorhynchus* in dry ice collections, but larvae were rarely found in rice fields. Ground pools other than rice fields were so scarce in this area that most adults may have been invaders from other areas. It is well known that this species has a very strong ability to fly (Horsfall, 1954 and so on).

Armigeres subalbatus (Coquillett): Adult females were attracted to baits from April to October. No distinct trends were recognized in the seasonal distribution, but a tendency of increase in September was recognizable. Larvae preferably breed in highly polluted water as in latrines, and no larvae were encountered in rice fields.

Culex halifaxii Theobald: Only one female was included in the collection at a pigsty. Larvae were rarely found in small ground pools with abundant organic matter in fallow or uncultivated rice fields near houses or pigsties. Available evidences suggest that the main blood source of this species is birds (Miyagi, 1972).

Culex hayashii Yamada: Larvae were collected in rice fields from April to October. In summer, the density tended to be higher in uncultivated fields than in cultivated ones. Many larvae were found in a large, stable and partly shaded ground pool at the foot of a hill, which may be a typical breeding place of the species. No females were attracted to baits. This species is considered to feed exclusively on frogs (Miyagi, 1972).

Culex infantulus Edwards: No adults were attracted to baits. Larvae were collected in rice fields but only after late June. The reason for this late finding is unknown. High density was observed in both cultivated and uncultivated fields. Miyagi (1973b) colonized this species and observed various interesting aspects of its biology, but the life in natural conditions is scarcely known.

Culex kyotoensis Yamaguti and LaCasse: Only two females were collected at pigsties, but there is no evidence of their having been attracted to pigs. Miyagi (1972) observed that a very small proportion of caged females feed on chickens, but nothing is known about the feeding habit in natural conditions. Larvae breed in containers of various types, and were not found in rice fields.

Culex bitaeniorhynchus Giles: Adult females were collected from April to October. The dry ice trap was much more effective than hand collection at pigsties, which may show that the species does not prefer pigs very much. Larvae, which preferably breed in the mass

Table 2. Numbers of mosquito larvae plus pupae collected in this study

1971	April			May				June			
	15	22	30	4	14	20	27	3	10	17	22
Anopheles hyrcanus group	57	19	8	2	2	2	2	29	42	179	157
Aedes vexans nipponii				4						1	1
Culex hayashii											
Culex infantulus											
Culex bitaeniorhynchus									4	64	14
Culex mimeticus group	5	4	13	3				1	4	10	
Culex pseudovishnui											
Culex tritaeniorhynchus			3	9	31	1	7	5	1	61	32
Culex vagans	3	1			20	8	4			1	

1972	April			May				June				
	13	21	27	4	11	18	25	1	8	15	23	29
Anopheles hyrcanus group	82	24	9	3	77	90	51	132	54	179	62	20
Aedes vexans nipponii									2			
Culex halifaxii												
Culex hayashii												
Culex infantulus											1	
Culex bitaeniorhynchus											3	
Culex mimeticus group	7	19	13	6	9	7	4	2	12	20	1	2
Culex pseudovishnui				1								
Culex tritaeniorhynchus	2	10	3	2	3	1	1	20	20	36	31	9
Culex pipiens pallens												
Culex vagans		1	1		1			14	5	1		

1973	April			May					June			
	5	19	26	4	10	17	24	31	7	14	21	28
Anopheles hyrcanus group	3	9	4	2	8	1	29	18	20	126	67	84
Aedes vexans nipponii											1	
Culex halifaxii												
Culex hayashii		1		1	1					1	4	2
Culex infantulus												1
Culex bitaeniorhynchus		1	2					1	1	26	37	
Culex mimeticus group	12	29	3	11	2		45	9	1	31	34	4
Culex pseudovishnui												
Culex tritaeniorhynchus	3	2	2	12			6	22	12	3	56	22
Culex pipiens pallens	1									1		1
Culex vagans		7	1	1	1	2	5	1				2

1974	April		May			June		
	18	25	2	14	29	5	13	20
Anopheles hyrcanus group	2		1	18	76	97	148	183
Aedes vexans nipponii							1	
Culex halifaxii								
Culex hayashii							1	1
Culex infantulus								1
Culex bitaeniorhynchus			1		1	4		5
Culex mimeticus group	5	2	7		10	3	5	5
Culex tritaeniorhynchus					1	24	19	26
Culex pipiens pallens								
Culex vagans				51	6	25		

* The census was given up halfway for the heavy rain.

Table 2. (Continued)

July					August			September					October				Total
1	9	15	26	31	9	17	27	3	8	16	22	29	5	13	20	28	
209	772	1390	73	291	108	61	30	50	51	162	193	143	60	25	11	1	4134
								3									9
1										1		2	2	1			7
				3						1	4						8
2	2																86
	3																43
	1	2		1													4
72	698	1180	29	437													2659
					64	3	15	4		5	2						37

July				August					September				October				Total
7	14	20	25	2	10	17	24	31	7	14*	21	28	4	11	18	25	
80	62	281	283	326	75	100	95	49	59		103	109	81	8	1	2	2496
																	2
												2	2				4
								2	11		3	6	2	3			27
						2	3	3	11		7		1	1			29
3	5	13	2	8		36		25			1	7				2	105
2									1							1	106
	1		2														4
5	16	68	93	318	36	38	26	5	71		15	41					870
												1	5	1			7
	1												3				27

July				August					September				October				Total
5	12	19	25	2	9	17	23	30	6	14	20	28	5	12	20	26	
483	1492	1370	620	337	139	54	68	50	20	34	114	186	114	62	14	8	5536
							2										3
											2						2
14	4	3	2	4	1	6		3		9	8	1					65
	3	15		2	14	5	21	2	2	2	2	7	1				77
4	33	3		430	15	6	5			2	2						576
16	12	4	3	1	1	1				2	28	22	2	1	1	2	277
1	3					2		1	2								9
302	1125	431	822	293	226	39	53	10	3	14	1	1	2				3462
												1	2				3
																	23

July				August				September				October		Total
4	11	18	25	1	8	20	29	5	12	19	26	9	24	
190	250	122	178	46	73	63	77	72	35	57	57	13	6	1764
														1
							8							8
2			5	1	3			5						18
1	1	1	3	2						2				11
		3	1											15
9	4												6	56
35	8	5	22	23	64	2	57	50	275	4				615
8	1													9
								1		1				84

Table 3. Numbers of female mosquitoes collected in this study

Species	By dry ice trap				By aspirator at pigsty			
	1971	1972	1973	1974	1971	1972	1973	1974
Anopheles lindesayi japonicus		1		2				
*Anopheles sinensis**	3748	1230	1956	1299	1549	533	850	710
Anopheles sineroides	5	5	6	5	2		1	
Aedes japonicus	1	1	6	4			2	1
Aedes nipponicus		1	3				1	
Aedes albopictus	3		1	5	2	2	1	
Aedes vexans nipponii	481	61	84	24	41	9	4	4
Armigeres subalbatus	65	30	52	77	59	31	80	63
Culex halifaxii							1	
Culex kyotoensis							1	1
Culex bitaeniorhynchus	180	37	69	35	7	3	1	1
Culex mimeticus			1	1				
Culex pipiens pallens	7	5	2	4	33	15	12	2
Culex pseudovishnui	7		4				4	
Culex tritaeniorhynchus	3964	623	659	824	1819	341	907	656

*A small number of *Anopheles lesteri* may be included.

of green algae, were found at least from April to October in rice fields. The seasonal distribution was rather irregular, but recognizable was a tendency of being abundant in June when the amount of green algae increases in ground pools in fallow fields.

Culex mimeticus subgroup: Three species were included. *Culex jacksoni* Edwards was encountered only once as a fourth instar larva. This was the first discovery of the species in our country (Mogi, 1978b). Immature stages of *mimeticus* Noè and *orientalis* Edwards were common in rice fields. They were found at least from April to October, but the number fell in the midsummer. Ito (1973) who colonized *orientalis* observed that it prefers chickens, lizards, mice and man in this order, but the feeding ecology in natural conditions is quite obscure. Only two females obtained at pigsties show that pigs are not preferable hosts.

Culex pipiens pallens Coquillett: This is the most common species inhabiting in or near human houses. Larvae were found in rice fields but only rarely in those near houses.

Culex pseudovishnui Colless: Both adults and larvae were uncommon. Wada *et al.*, (1967) collected surprisingly numerous females by dry ice traps in the same area in 1965 (under the name of *Culex vishnui*). The year must have been an unusual one for the species in this area.

Culex vagans Wiedemann: Immature stages were collected from spring to early summer and less frequently in autumn. In early summer, larvae were not rare in fallow fields, but adults were never attracted to baits. Natural feeding habits are obscure.

Culex tritaeniorhynchus Giles: This is a dominant mosquito next to *Anopheles sinensis*. The population of the species will be analized at length in the following sections.

5. The Developmental Period of *Culex tritaeniorhynchus*

Knowledge on the developmental period is indispensable to study animal populations. In poikilotherms such as insects, the developmental speed is influenced most profoundly by the temperature. When such multivoltine species as *tritaeniorhynchus* with short generation time occur in the temperate region, the developmental period varies greatly following the seasonal change of temperatures. Therefore, it would be reasonable to formulate the effect of temperatures first.

The relation of the temperature (t) to the developmental period (D) or the developmental speed ($V=1/D$) of poikilotherms is well known to be expressed by the law of constant heat summation as follows :

$$D=K/(t-t_0) \qquad \cdots\cdots (1)$$

or

$$V=(t-t_0)/K \qquad \cdots\cdots (2)$$

where t_0 is a threshold temperature for development (a developmental zero point) and K is a thermal constant. In this paper, D is expressed in days and t means a daily mean temperature.

The mean developmental period may be calculated most precisely from the frequency distribution of developmental periods. In this study, however, a convenient method was adopted, its procedure being as follows. The age structure was observed for a group of insects at a regular time interval (usually one day), then the duration from the time when one stage reaches 0.5 of survivors to that when the next stage does was regarded as the developmental period of the former stage.

5.1 The Developmental Period of Eggs

Egg rafts, which were obtained at the air temperature of 27°C, were moved to insectaries with various temperatures within two hours after being laid. The observed period of eggs (D_E) and its reciprocal (V_E) are shown in Fig. 8. Their relation to air temperatures (t_a) can be expressed by the following equations.

$$V_E=(t_a-9.6208)/22.1729 \qquad \cdots\cdots (3)$$

$$D_E=22.1729/(t_a-9.6208) \qquad \cdots\cdots (4)$$

The hatch of *Culex* eggs is not delayed by diapause or by desiccation. Therefore, the developmental period is expected to be determined exclusively by the temperature. However, the temperature itself may influence the egg duration in a complicated manner, especially in the field, because radiant heat may be effective besides air temperatures. Possibly, radiant heat affects the development of eggs through both or either of two ways, that is, by raising the temperature of the water surface on which egg rafts float and/or by heating eggs directly. These effects, however, do not appear very important for the present study by the following reasons. Firstly, the egg duration is generally so short that the effect, if any, can not be accumulated greatly, especially in summer. Secondly, egg rafts are pulled to stems of rice plants or to other objects by the action of surface tension, which must reduce their chance

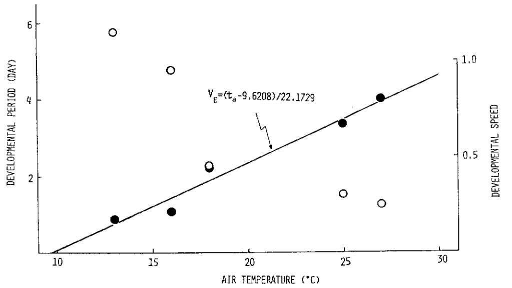

Fig. 8. Relation of the developmental period (hollow circle) and speed (solid circle) of *Culex tritaeniorhynchus* eggs to air temperatures.

to be exposed to direct sunlight. Thus, it is considered that Equation (4) is applicable to obtain rough estimates of the egg duration in the field.

5.2 The Developmental Period of Larvae

The developmental period of larvae is strongly influenced by the amount of food in addition to the water temperature. Also, the effect of variable temperatures must be examined, because variable temperatures are known to accelerate the development of insect larvae including mosquitoes (Huffaker, 1944). Considering these points, four series of experiments were done.

Series	Place	Temperature	Food
A	Indoor insectary	Constant	Artificial
B	Outdoor insectary	Variable	Artificial
C	Fallow field	Variable	Natural or Artificial
D	Rice field	Variable	Natural or Artificial

The "artificial" food means that a sufficient amount of the mixture of ground mouse pellets and dried yeast was supplied. In (B), larvae were reared in enamel pans exposed to direct sunlight. In (C) and (D), larvae were reared in nets suspended into water from floats on the water surface. For a part of replicates in (C) and (D) (natural food), nets with larger meshes were used following the advance of instars to keep the water in nets as natural as possible by the exchange of water through meshes. For the other part of replicates (artificial food), used were nets with meshes sufficiently small to keep the added food until the next supply. In (B), (C) and (D), the maximum and minimum temperatures at 1 cm below the water surface were recorded by fixing a thermometer to the underside of floating boards. The daily mean temperature calculated from them, therefore, is considered to represent well the water temperature in the microhabitat where larvae spend most their time. The mean temperature during larvae (or pupae) was obtained by averaging daily mean temperatures during the period when they had developed. Results of these experiments are presented in Tables 4, 5, 6, 7 and Fig. 9.

The developmental period varied often considerably even among replicates in the indoor insectary with a constant temperature and ample food. Probably it was due to the

Table 4. Developmental periods of immature stages of *Culex tritaeniorhynchus* under constant temperatures in the laboratory

Water Temperature (°C)	Mean developmental period (day)					
	L1	L2	L3	L4	Larva	Pupa
28	1.31	0.84	0.98	2.19	5.32	1.84
28	1.16	0.99	1.00	2.28	5.43	1.74
28	1.31	0.84	0.98	2.19	5.32	1.84
25	1.58	2.07	1.75	2.20	7.60	1.81
25	1.58	2.35	1.58	2.03	7.54	1.51
25	2.05	1.38	1.37	2.34	7.14	
22	1.81	2.30	2.65	3.97	10.73	2.10
22	2.10	2.12	2.05	2.83	9.10	1.91
22	2.10	2.03	2.14	2.81	9.08	1.71
19	2.59	2.04	3.45	3.72	11.80	2.10
19	2.59	2.14	3.05	4.30	12.08	2.00
16	3.66	4.04	5.35	9.55	22.60	
16	3.92	4.20	4.78	7.84	20.74	3.84

Table 5. Developmental periods of immature stages of *Culex tritaeniorhynchus* under variable temperatures at the outdoor insectary

Date of hatch	Mean water temperature during larval development(°C)	Mean period of larval development (day)					Mean water temperature during pupal development(°C)	Mean period of pupal development (day)
		L1	L2	L3	L4	Total		
6 May 1972	22.5	1.47	1.50	1.13	3.75	7.85	22.2	2.13
9 Jun. 1972	25.5	0.94	2.20	1.85	2.25	7.24	26.4	2.04
3 Jul. 1972	27.3	1.97	1.02	1.03	1.88	5.90	27.2	1.85
28 Jul. 1972	29.2	0.71	0.95	1.08	2.63	5.37	29.4	1.87
28 Sep. 1972	21.7	2.78	1.27	1.00	4.71	9.76	22.9	2.48
23 Mar. 1973	17.3	7.00	2.20	2.80	7.75	19.75	18.0	3.75
25 Apr. 1973	21.1	3.05	3.00	2.98	4.17	13.20	20.9	2.06
11 Jul. 1973	31.6	1.00	1.00	1.03	2.04	5.07	32.3	1.93

Table 6. Developmental periods of immature stages of *Culex tritaeniorhynchus* in fallow fields

Date of hatch	Mean water temperature during larval development(°C)	Supply of food	Mean period of larval development (day)					Mean water temperature during pupal development(°C)	Mean period of pupal development (day)
			L1	L2	L3	L4	Total		
28 Apr. 1972	22.1		3.83	3.31	3.46	4.30	19.40		
28 Apr. 1972	23.0		3.39	2.38	3.82	4.88	14.47		
28 Apr. 1972	22.4		3.53	2.72	3.37	4.85	14.47		
26 Apr. 1973	22.5	+	2.78	1.95	2.35	4.25	11.33		
26 Apr. 1973	19.5	+	3.36	3.42	2.00	4.22	13.00		
26 Apr. 1973	22.9	+	2.78	2.00	1.28	4.18	10.24		
26 Apr. 1973	21.9	+	2.78	2.00	2.75	4.25	11.78		
26 Apr. 1973	22.2	+	2.78	1.92	1.99	4.09	10.78	21.9	2.33
26 Apr. 1973	22.5		2.78	2.14	1.98	5.96	12.86		
26 Apr. 1973	21.9		2.78	2.15	2.02	4.58	11.53		
26 Apr. 1973	22.2		2.78	1.95	2.12	4.76	11.61		
27 Apr. 1974	22.6		3.58	3.07	2.25	4.91	13.81	24.6	2.35
27 Apr. 1974	22.1		4.82	2.82	2.45	4.41	14.50	23.8	2.00
27 Apr. 1974	22.3		3.95	3.63	2.34	4.25	14.17	23.7	1.60

Table 7. Developmental periods of immature stages of *Culex tritaeniorhynchus* in cultivated rice fields

Date of hatch	Mean water temperature during larval development(°C)	Supply of food	Mean period of larval development (day)					Mean water temperature during pupal development(°C)	Mean period of pupal development (day)
			L1	L2	L3	L4	Total		
3 July 1972	30.7		1.76	0.58	0.69	2.02	5.05		
3 July 1972	30.7		1.08	1.01	0.77	1.60	4.46		
3 July 1972	30.4		1.32	1.36	1.66	2.82	7.16		
28 July 1972	30.9		1.05	1.00	0.98	2.37	5.40		
28 July 1972	31.0		1.05	1.30	0.87	2.21	5.43		
28 July 1972	30.7		1.77	1.30	1.58	4.43	9.08		
28 July 1972	30.8		1.11	1.84	1.05	2.73	6.73		
9 July 1973	30.3		1.02	0.98	1.00	1.83	4.83	29.3	1.95
9 July 1973	30.9		1.00	1.00	1.00	1.73	4.73	30.4	1.77
9 July 1973	31.6		1.00	1.13	1.23	1.74	5.10	32.3	1.96
9 July 1973	31.7		1.02	1.14	1.34	1.74	5.24	32.4	1.96
9 July 1973	31.8		1.00	1.62	1.26	1.87	5.75	32.4	1.37
9 July 1973	29.8		1.05	1.11	1.45	2.51	6.12	30.6	1.88
9 July 1973	29.1		1.03	1.00	0.97	2.07	5.07	29.4	2.00
9 July 1973	30.4		1.00	1.00	1.00	1.80	4.80	31.0	1.95
9 July 1973	29.9		1.00	1.00	1.00	1.95	4.95	28.9	1.98
9 July 1973	29.7		1.00	1.00	1.03	1.93	4.96	29.2	1.96
9 July 1973	30.3	+	1.00	1.00	1.03	1.73	4.76	29.3	1.99
9 July 1973	30.9	+	1.05	1.01	1.00	1.86	4.92	30.6	1.96
9 July 1973	31.6	+	1.02	1.00	1.01	1.57	4.60	32.3	2.00
9 July 1973	31.7	+	1.02	0.98	1.00	1.26	4.26	31.8	2.00
9 July 1973	31.7	+	1.02	1.11	0.94	1.83	4.90	32.2	2.00
9 July 1973	29.2	+	1.02	1.01	1.07	1.90	5.00	30.0	1.91
9 July 1973	29.0	+	1.02	1.00	1.00	1.40	4.42	29.3	2.02
9 July 1973	30.6	+	1.00	1.00	1.00	1.16	4.16	30.1	1.97
9 July 1973	30.3	+	1.00	1.00	1.00	1.44	4.44	28.2	2.00
9 July 1973	29.7	+	1.02	1.00	0.98	1.53	4.53	29.2	2.00

retardation of development in a part of replicates by the growth of the unsuitable biota (micro-organisms) or physical conditions hard to be controlled. Therefore, the shortest period among replicates was regarded as a standard at the constant temperature with sufficient food. Thus, the regression equation of the developmental speed (V_L) to the water temperature (t_w) at the constant temperature with sufficient food was obtained as follows.

$$V_L=(t_w-11.8036)/89.2857 \quad \cdots\cdots \quad (5)$$

It can be rewritten as,

$$d_L=89.2857/(t_w-11.8036) \quad \cdots\cdots \quad (6)$$

where d_L is the developmental period of larvae under the constant temperature with sufficient food.

As for the developmental zero point of *tritaeniorhynchus* larvae, two reports are available. Wada and Omori (1971) stated that larvae hardly develop at the air temperature of 16

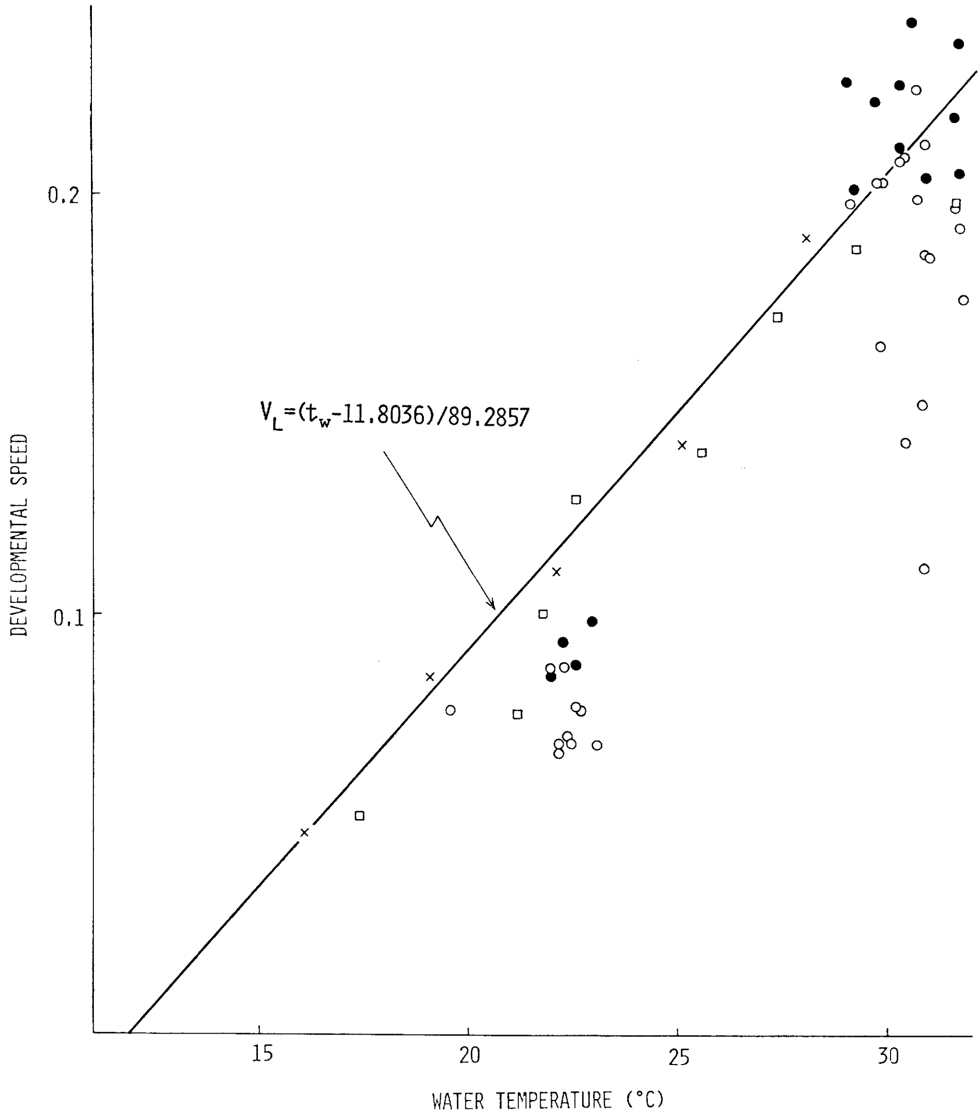

Fig. 9. Relation of the developmental speed of *Culex tritaeniorhynchus* larvae to water temperatures. × : laboratory with constant temperatures. Square : outdoor insectary with variable temperatures. Hollow circle : rice field (natural food). Solid circle : rice field (artificial food was supplied).

°C. Provided that the water temperature is lower than the air temperature by 2°C, the actual temperature for extremely slow development would be regarded as about 14°C, which is still higher than the value obtained here. As it is, their data show that larvae can develop at lower air temperatures than 16°C. On the other hand, Yoshida *et al.* (1974) obtained 8.3°C being much lower than the present value. The main source resulting in this discrepancy is shorter developmental periods at low temperatures in their experiments. Therefore, shorter developmental periods than present ones may be obtained if the number of replicates is increased. However, it is preferred to go forward, leaving the problem to the future study, because the present aim is not to know t_0 or K as precisely as possible but to get a base for estimating the developmental period in the field.

Comparing the value based on Equation (5) with the developmental speed obtained in other series of experiments, the following facts can be understood. Firstly, the acceleration of development by variable temperatures is negligible, if any. Secondly, the developmental period in the field can be shortened by adding food to natural water, which means that the amount of food is frequently insufficient in the field for larvae to grow at the maximum speed. On an average, the developmental period in natural food conditions was 1.4 times (the range 0.93–1.92) as long as the value expected from Equation (6). It is highly probable that this difference between real values and ideal ones varies from season to season in a predictable manner (see Section 6.6.8). However, there are no sufficient data at present to incorporate this factor in the equation, therefore the average value 1.4 was adopted for all seasons. Thus, the developmental period of larvae in the field (D_L) can be expressed as follows.

$$D_L=1.4\cdot d_L \quad\cdots\cdots\cdots \quad (7)$$

For population analyses, it is highly desirable that the developmental period of each instar is available. It can easily be calculated from Equation (7), provided that the proportion of each instar period to the whole larval period is constant irrespective of temperatures. Fortunately, this premise met the fact (Fig. 10). The first, second and third instars occupy about 0.2 of the whole larval period, respectively, and the fourth instar does about 0.4 irrespective of temperatures. Therefore, the approximate period of the n-th instar (D_{Ln}) in the field can be obtained from the following equation.

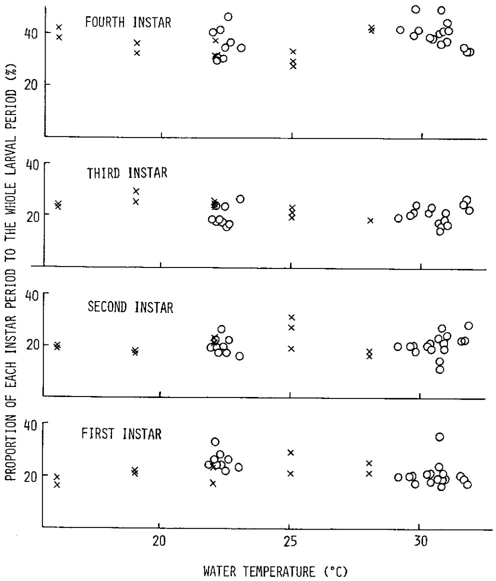

Fig. 10. Proportion of each instar period to the whole larval period. × : laboratory with constant temperatures. Circle : rice field with variable temeratures.

$$D_{Ln}=1.4\cdot d_L\cdot k \qquad (8)$$

where k is 0.2 when n is 1,2,3, and 0.4 when n is 4.

The water temperature is, however, unavailable from usual meteorological tables. Therefore, it is convenient to express Equations (7) and (8) in terms of air temperatures obtainable from the nearest meteorogical station. To do this modification, the relation between the daily mean water temperature in rice fields in the study area and the daily mean air temperature observed at Nagasaki Marine Observatory was examined. As seen from Fig. 11, the former was almost always higher than the corresponding latter. Of course, a small part of this difference may be attributable to the local variation of temperatures, but the main part is due undoubtedly to the difference of microhabitats, that is, the air at 1.5 m above the earth and the surface water of shallow and open pools. In the latter, the maximum temperature is greatly risen by radiant heat. The extent of difference between the two mean temperatures was exceedingly variable, ranging from nothing to 7°C. One factor responsible for this variation is the variation in daily hours of sunshine. In fact, a weak correlation was recognized between the temperature difference and hours of sunshine. Also, conditions in and around each rice field, for instance, the source of water, the manner of water management, vegetation and topography, must be very important. For more detailed studies, these factors may be considered. In this study, however, the constant temperature difference of 3.5°C was adopted for convenience sake.

$$t_w=t_a+3.5 \qquad (9)$$

By putting Equations (6) and (9) into (7) and (8), we can get following equations.

$$D_L=125/(t_a-8.3036) \qquad (10)$$

$$D_{L1}=D_{L2}=D_{L3}=25/(t_a-8.3036) \qquad (11)$$

$$D_{L4}=50/(t_a-8.3036) \qquad (12)$$

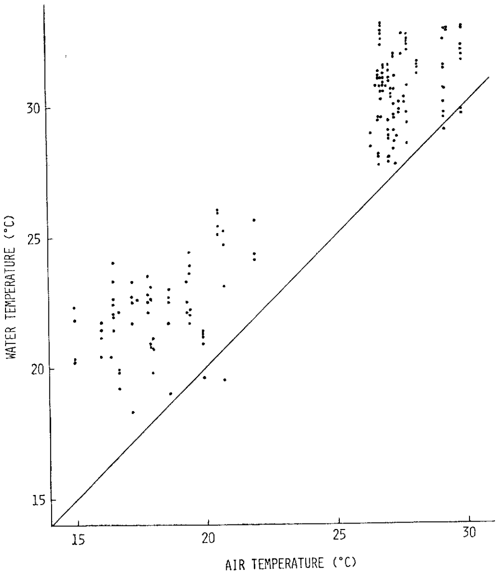

Fig. 11. Relation between the water temperature in rice fields and the air temperature

5.3 The Developmental Period of Pupae

Developmental periods of pupae (D_P) at various conditions are included in foregoing Tables 4, 5, 6 and 7. They are not influenced by the amount of food, at least directly, therefore the dominant influence of temperatures was expected. Nevertheless, no clear correlation was recognized between the developmental speed of pupae (V_P) and the water temperature (Fig. 12). Probably this is due to the circadian rhythm in both pupation and emergence. Khan and Reisen (1977) observed with *tritaeniorhynchus* that both pupation and emergence begin in the afternoon with a peak around dusk. It means that emergence from pupae which have matured in the morning is suspended until the following evening. If this is the case, the pupal period in days may take values near integers such as 2, 3 and 4, and the developmental speed is expected to be rather constant in a range of temperatures and to jump from a level to another without gradation. In fact, such a tendency is recognizable in Fig. 12. V_P was about 0.5 (D_P was about 2 days) in the range of temperatures from 20°C to 30°C. At lower or higher temperatures, observations were so few as to examine the above assumption, although some values in those ranges were extremely small or large. However, the evidence is still not enough to accept the assumption as the ground for estimating the pupal period. Therefore, an equation was derived following the law of constant heat summation for convenience sake.

$$D_P=99.0099/(t_a+25.1733) \quad \cdots\cdots(13)$$

Values obtained at constant temperatures were excluded from the calculation, because they are distant from values obtained under fluctuating temperatures. It may be due to the weakened circadian rhythm under constant temperatures. Of course, Equation (13) is so superficial that no biological meanings should be given to it.

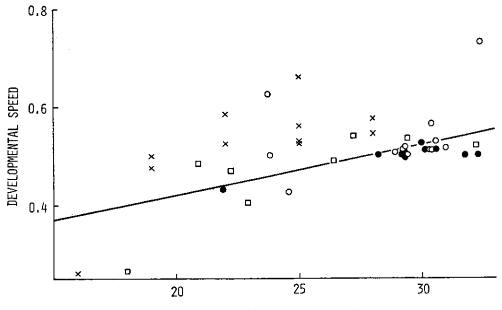

Fig. 12. Relation between the developmental speed of *Culex tritaeniorhynchus* pupae and the water temperature. For symbols, see Fig. 9.

5.4 The Period from Emergence to the First Oviposition

This part is based on data kindly offered by Dr. Wada (Fig. 13). The relation of the reciprocal of this period (V_A) and the air temperature (t_a) is,

$$V_A=(t_a-12.4513)/88.4956 \quad \cdots\cdots(14)$$

thus,

$$D_A=88.4956/(t_a-12.4513) \quad \cdots\cdots(15)$$

It seems probable that the data were obtained in not very good conditions. Judging from other fragmentary observations, the period can possibly be shortened, especially at low temperatures. The minimum temperature to produce eggs successfully may be about 10°C or lower. Therefore, the bias may be considerably large at low temperatures. However, at temperatures above 20°C, the bias is considered to be small. In addition, oviposition may be delayed in the field by various external factors. Bad weather such as a strong wind or heavy rains may inhibit the flight which is a prerequisite to find hosts or suitable collections of water. Further, the direction of flight is random in relation to hosts or breeding places until mosquitoes happen to enter the narrow range where the orientation to objects is possible. Therefore, two or more nights may pass before the object is encountered. Considerable deviation from the estimate based on temperatures are highly probable. In view of these points, it is considered that Equation (15) can be used for calculating rough estimates of the duration in the field except for the very early season.

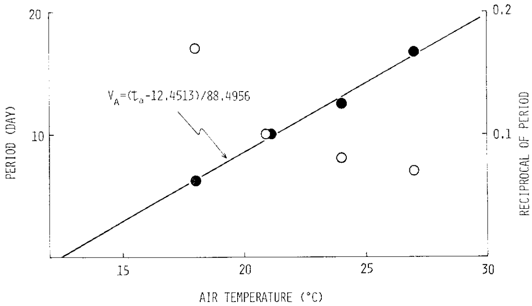

Fig. 13. Relation of the period from adult emergence to the first oviposition (hollow circle) and its reciprocal (solid circle) to air temperatures, based on data offered by Dr. Y. Wada.

5.5 A Summary on the Developmental Period of *Culex tritaeniorhynchus*

Estimated periods of each stage at various air temperatures are presented in Table 8. There were excluded values at low temperatures where the error is considered to be relatively

Table 8. Estimated periods of each stage of *Culex tritaeniorhynchus* in the field

Stage	Period (day) when air temperature (°C) is												
	18	19	20	21	22	23	24	25	26	27	28	29	30
Egg	2.65	2.36	2.14	1.95	1.79	1.66	1.54	1.44	1.35	1.28	1.21	1.14	1.09
First instar	2.58	2.34	2.14	1.97	1.83	1.70	1.59	1.50	1.41	1.34	1.27	1.21	1.15
Second instar	2.58	2.34	2.14	1.97	1.83	1.70	1.59	1.50	1.41	1.34	1.27	1.21	1.15
Third instar	2.58	2.34	2.14	1.97	1.83	1.70	1.59	1.50	1.41	1.34	1.27	1.21	1.15
Fourth instar	5.16	4.67	4.27	3.94	3.65	3.40	3.19	2.99	2.83	2.67	2.54	2.42	2.30
Pupa	2.29	2.24	2.19	2.14	2.10	2.06	2.01	1.97	1.93	1.90	1.86	1.83	1.79
Pre-oviposition*	15.95	13.51	11.72	10.35	9.27	8.39	7.66	7.05	6.35	6.08	5.69	5.35	5.04
Total	33.79	29.80	26.74	24.29	22.30	20.61	19.17	18.95	16.87	15.95	15.11	14.37	13.67

*Adult emergence to the first oviposition large. Even in the range from 18°C to 30°C, the developmental period varies greatly according to temperatures. In the midsummer, one life cycle is expected to be completed within two weeks, but it probably requires about one month in late spring or early summer.

6. Population Studies on *Culex tritaeniorhynchus*

6.1 Basic Procedures to Arrange the Data

Before going further, it would be justifiable to explain the fundamental plan to arrange the data collectively.

6.1.1 Larvae and pupae

The original data are the number of each developmental stage in a dip and the rate of the water-logged area, both recorded for each rice field. The number per dip is a kind of relative density. It is the most convenient and popular expression of density in population studies on larval and/or pupal mosquitoes. Various information on the population can be obtained through it, therefore it is good enough for a particular purpose, especially for a practical one.

Absolute density is, however, indispensable for population studies of more advanced stages. Therefore, the efficiency of the dipper to collect *tritaeniorhynchus* in rice fields was examined, and one larva or pupa per dip by the dipper of our use proved to be, on an average, equivalent to 186 larvae and/or pupae per m^2 of the water surface of rice fields (Wada and Mogi, 1974). Therefore, the total number in the study area would easily be calculable by the following procedure if the water-logged area were constant through all the rice fields.

$$\textit{Total No. in the study area} = \textit{Average No. per dip} \times 186 \times \textit{Total area with water in } m^2 \quad \cdots\cdots (16)$$

As it is, however, water-logged area is highly variable among rice fields. The water-logged area in each rice field depends on both the total area of the rice field and the rate of the area with water. As stated already (see Section 2), the area of one rice field was 300 m^2 on an average. Here we assume that the area of each rice field is equally 300 m^2. Strictly speaking, this assumption is inconsistent with the fact, the largest rice field in the study area being ten or even more times as large as the smallest one. However, this variation is considered to be cancelled if a sufficiently large number of rice fields are examined, since no correlation was found between the area of each rice field and the density of mosquitoes there. As a matter of fact, it is very difficult work costing much labor and time to measure the area of each rice field, in such a place as the study area where most rice fields are strongly irregular in shape under the influence of complicated micro-topography. The rate of the water-logged area, on the other hand, varies from rice field to rice field more drastically (from 0 to 1.0) except for cultivated fields in a short period following transplanting (see Sections 3, 6.6.7). Besides, the water-logged rate of each rice field has a close correlation with the mosquito density per unit area of water in each rice field. Any student who has ever been concerned with field studies on mosquitoes breeding in ground pools would not hesitate to recognize that higher density is encountered more frequently in smaller pools. In these circumstances, Equation (16) would tend to give an overestimation of the total number in the area. Correction or weighting of some kinds is necessary. The procedure adopted here is expressed in Equation (17).

$$\textit{Total No. in rice fields examined} = \{\sum(\textit{No. per dip} \times \textit{Water-logged rate})\} \times 186 \times 300 \quad \cdots\cdots(17)$$

As 200 rice fields out of 500 were examined, the total number in the study area can be obtained as the below.

$$\textit{Total No. in the study area} = \textit{Total No. in rice fields examined} \times 2.5 \quad \cdots\cdots(18)$$

Of course, the procedure can be applied to each developmental stage of mosquitoes and/or each rice field group based on types, locations and so on. In this paper, the total number of each stage was calculated for two types of rice fields, that is, cultivated fields and uncultivated ones.

The age structure thus obtained is, however, an apparent one, since the developmental period varies not only from stage to stage but also from season to season. Further correction is indispensable for further analyses of populations, for instance, to estimate the survival rate. The developmental period in rice fields is obtainable from Table 8 if air temperatures are available, thus,

$$\textit{Total No. of each stage at the median time of the stage} = \textit{Total No. of each stage in the study area} \,/\, \textit{Mean period of the stage at the then temperature} \quad \cdots\cdots(19)$$

Ten-day average temperatures were used here, and the resultant age structure is shown in Table 9, which will be discussed at length in later sections.

6.1.2 Adult females

One dry ice trap collection and two hand collections at pigsties are available on each census day as a rule (see Section 2). Strictly speaking, females attracted to pigs are slightly older in physiological age (having slightly larger follicles) than those attracted to dry ice (Yajima, 1975). However, both the groups take blood easily if suitable hosts are available. Therefore, both of them were considered to represent the female population capable of taking blood in the night. As is generally known, the seasonal distribution of female *tritaeniorhynchus* attracted to baits varies from place to place even in the same village or rice field area, owing probably to the strong bias in both distribution and direction of flying mosquitoes (Ishii and Karoji, 1976). Therefore, the more the number of collection sites, the more precisely the seasonal distribution in the area can be assessed. It means that the best information on the seasonal distribution of females is obtainable by averaging or totalling all the available samples. In this study, however, two sampling methods with different efficiency were employed, so it would be wise to correct the data before averaging or totalling. Generally speaking, the number collected at pigsties is more convenient to discuss the abundance of females in relation to both the population dynamics of the species and the epidemiology of JE. Thus, the number of females collected by a dry ice trap (*DIT*) was converted to the number collected at

Table 9. Age structure of immature stages of *Culex tritaeniorhynchus* in the study area

Date	Total No. in the study area at the median age of each stage (10^3)									
	Cultivated field					Uncultivated field				
	L1	L2	L3	L4	Pupa	L1	L2	L3	L4	Pupa
1971										
Apr. 30		4	21	2				24	10	
May 4		29	136	22	53					
14		12	49	660	118					
20			48							
27			52	173						
Jun. 3			124	131	62					
10				71						
17		38	916	1029	342					
22	161	123	1170	317	21					
Jul. 1	1450	472	785	928	375	959	210			
9	36122	22479	10759	4580	600	33	22	77		
15	30459	29817	26895	7013	825	22	1			
26		253	406	1433	274			1		
31	5119	12681	19107	8919	75		2	33		
Aug. 9	439	747	1120	1736	225		9	34	68	
17				198						1
27			271	5					13	
Sep. 3		88								
8										
16	70	167	219	88						
22	82			78						
Total	73902	66910	62078	27358	2970	1014	244	169	91	1
1972										
Apr. 13	43									
21	227	120								
27			69							
May 4			60	27						
11			92							
18	49									
25	2									
Jun. 1	191	202	782	34	62					
8	248	135	205	4						
15	526	1	321	169	33					
23	512	746	281	512						
29		88	614	44						
Jul. 7	124			35	72				2	
14	336	99		39	83				32	
20	3260	945	1182	306	43		122			
25		1428	1087	1510	150	34	55	66	33	
Aug. 2	1848	2020	1921	2939		1173	37	161	89	1
10	416	104	104	366	73	2	3	5	6	
17	208	468	157	204		115		158	19	
24	725	102	163	42		409				
31		93	186	42					47	
Sep. 7	1603			5		82	112			
14										
21		59				137	160	1		
28							20	132	37	2
Total	10318	6610	7224	6278	511	1959	509	523		3

pigsties as follows.

Weighted No. per DIT = No. per DIT × (Annual Total No. per pigsty/Annual Total No. per DIT) ……………………………………………………………(20)

where annual totals include only the collection on the day when both the methods were used. Then, three samples (two at pigsties and one by a dry ice trap) were averaged.

Table 9. (Continued)

Date	Total No. in the study area at the median age of each stage (10^3)									
	Cultivated field					Uncultivated field				
	L1	L2	L3	L4	Pupa	L1	L2	L3	L4	Pupa
1973										
Apr. 5	8									
19				19			2	19		
26										
May 4								27	108	92
10										
17										
24		24	107					48		
31	17	155	54	48	62					
Jun. 7		183	91	62	153					
14				70						
21	123	1167	1044	389	62		7			
28		684	583	186	69					
Jul. 5	1477	6426	5204	3951	687	2681	2958	2523	311	116
12	20963	15043	15477	4171	450	3171	181	1		4
19	13747	5141	3032	1513	1125	1757	733	401	122	1
25	2318	5311	1417	659	150	1875	1566	3127	1000	338
Aug. 2	967	220	1637	110		297	1477	1186	795	68
9	1285	330	648	165		3535	46	98	22	14
17	115	219	127	46			14	215	36	
23	1593	165		55		137		5	2	
30			110			108	115		157	
Sep. 6			88	47			1			
14	76					30	84	152	31	
20	76									
27		7								
Oct. 4				2			4			
Total	42765	35075	29619	10754	2758	13593	7188	7802	2578	633
1974										
May 29				23						
Jun. 5		46	70	176						
13	14	113	193	35	13					
20	412	156	124	25						
Jul. 4	353	795	465	280		1	2	1	2	
11	93	558					56			
18			89	20		1		1	30	
25	594	495	396	345						
Aug. 1	104	354		52		12	2	3		
8	208	729	416	104		1	32	140	4	
20				104						
29	104		208	52		36	23	97	21	34
Sep. 5						85	84	37	7	4
12						436	87	49	28	20
19									2	
Total	1882	3246	1960	1216	13	592	285	328	94	58

6.2 Seasonal Prevalence of *Culex tritaeniorhynchus*

Seasonal prevalence of the average number of larvae plus pupae per m^2 (based on the unweighted average per dip) is shown in Fig. 14. It is quite clear that density is generally much higher in uncultivated fields than in cultivated ones. The highest average density in uncultivated fields was 5636 per m^2 (30.3 per dip) on July 25, 1973. The average density over 500 per m^2 was not rare. In contrast with it, the maximum in cultivated fields was 1169 per m^2 recorded on July 14, 1971. It is only about one fifth of the maximum in uncultivated fields. The average density exceeded 500 per m^2 only twice.

Also, a tendency is clearly seen that the average density in uncultivated fields reaches high levels frequently in late summer or early autumn. Such a tendency was not observed in cultivated fields, where high density occurred almost exclusively in the midsummer.

Next, we will examine the seasonal distribution of the total number of larvae plus pupae which is shown also in Fig. 14. As seen clearly, the total number was much larger in cultivated fields in spite of much higher density per m^2 in uncultivated fields. This inversion is attributable to the difference in the water-logged area. Cultivated fields were at least four times as many as uncultivated ones in number, being more than ten times in 1971 (Table 1). Also, the rate of the water-logged area in the former was usually more than ten times as high as the latter in the midsummer (Fig. 7). Thus, the overall water-logged area in cultivated fields was usually more than fifty times, frequently more than a hundred times, as large as that in uncultivated ones, being sufficiently large to cancell the higher density per unit area in the latter. In fact, the general feature of the seasonal prevalence in the study area was determined largely by the prevalence in cultivated fields. The total number reached its yearly

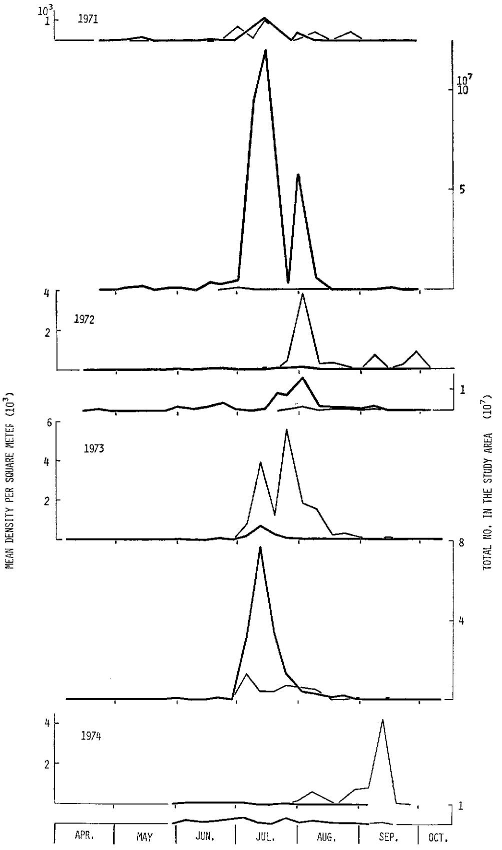

Fig. 14. Seasonal prevalence of *Culex tritaeniorhynchus* larvae plus pupae in the study area. Mean density per m^2 (upper) and the total number in the study area (below) are shown for each year. Thick line : cultivated field. Thin line: uncultivated field.

peak in July or early August except for 1974 when the population was extremely small. It can be concluded that this peak in cultivated fields was resulted from the increase in both water logged area and density per unit area.

However, factors responsible for the yearly change in the size of summer populations are not necessarily clear from present data. It seems that there is a positive correlation between population levels in summer and the temperature from July to early August (see Fig. 3), especially the synchronization of the very small population and the very low summer temperature in 1974 being conspicuous. However, the yearly difference in ten-day average temperatures of summer was within 3°C, which alone is too small to explain the large fluctuation in the population size, since the distinct change in survival and/or reproduction rates is hardly expected to be caused by the temperature difference of this scale at least in the range from 25°C to 30°C. The effect of temperatures will be referred to again in the next paragraph.

Also, an inverse correlation between the population size in summer and the amount of precipitation in early and middle July is suggested (see Fig. 7). The precipitation in this season was large both in 1972 and 1974 when the population was small. Effects of rainfalls can be both direct and indirect. The direct effect is to wash away the aquatic stages. This effect can be serious enough to result in a sudden and sharp drop in the population. A typical example was experienced in late July in 1971 when the heavy rain lasted for several days. On July 26 when the delayed census was done following the stop of the rain, water was overflowing from many rice fields into the river *via* ditches, and larvae were very scarce. Also, it was found that dispersal rates of *tritaeniorhynchus* larvae by water currents are considerable even when water currents in rice fields are kept normal through the management by farmers. Therefore, the direct effect of rainfalls is considered to be very important, especially in the terraced rice field area being common in Nagasaki. Rainfalls can influence *tritaeniorhynchus* larvae indirectly, too. They replace the water containing plentiful food with clean water. This effect may be significant in certain circumstances, because the amount of food is insufficient frequently in rice fields (see Section 5.2). Another indirect effect of rainfalls is considered to be more profound. As presented earlier (Fig. 11), the raise of temperatures by radiant heat is very large. This effect, however, would hardly be produced on heavily rainy days, when water temperatures may even be lower than air temperatures. Thus, there may be produced the difference of 5°C between the mean water temperature of continuous shiny days and that of continuous rainy days. As seen a little earlier, ten-day-average temperatures in summer change yearly within about 3°C. Therefore, when low air temperatures are accompanied with heavy rains, the resultant fall of water temperatures may even approach 10°C, as compared with the summer with the reverse combination of the meteorological factors. The temperature difference of this scale would result in a considerable difference in survival rates of aquatic stages through the prolonged developmental period (see Section 6.6.1). Thus, rather small differences in air temperatures should not be underestimated when their effects on *tritaeniorhynchus* populations are considered. In fact, meteorological data in the past show that cold summer in Japan is often accompanied with rainy days. Thus, two meteorological factors, that is, temperature and precipitation in summer, are considered to be very important factors to determine the population size of *tritaeniorhynchus* in summer. The positive correlation between the number of adult *tritaeniorhynchus* and the summer temperature was found also in Osaka (Buei *et al.*, 1978) and Miyagi (Kato, 1968), both in Japan.

Seasonal prevalence of median-aged pupae is shown in Fig. 15, with that of adult females attracted to baits. In principle, seasonal prevalence was similar in pupae and adults, both the populations reaching yearly peaks in the midsummer except for 1974. This tendency in the seasonal prevalence of adult *tritaeniorhynchus* in Japan has been confirmed repeatedly since the pioneer work by Yamada (1933)*. Strictly speaking, however, not a few dissimilarities were found. This may be explained partly by the biased distribution of flying mosquitoes and the bad weather in the evening when adults were collected but largely by migration of adult

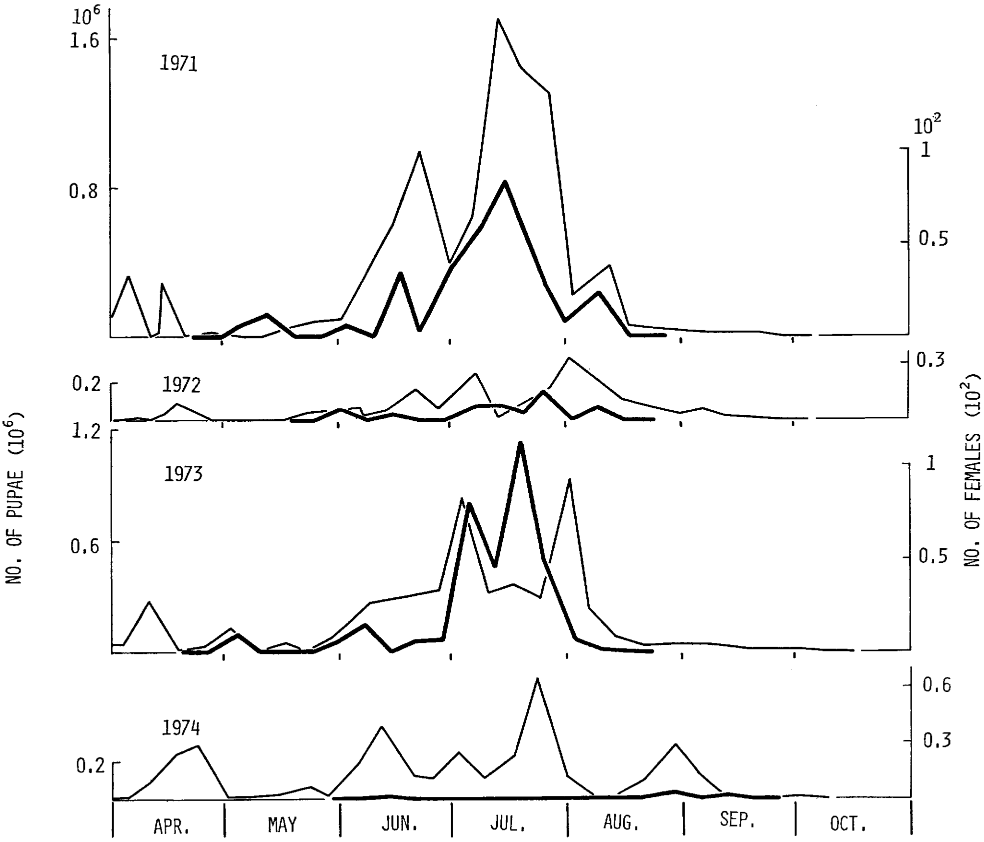

Fig. 15. Seasonal prevalence of pupae and adult females of *Culex tritaeniorhynchus* in the study area. Thick line: total number of median-aged pupae in the study area. Thin line: number of adult females collected per man per 10 minutes per pigsty.

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* Incidentally, this midsummer peak is known as "Yamada's peak" to Japanese medical emtomologists.

females into or from the study area. For further discussion on adult migration, see following Sections 6.4, 6.5 and 6.6.17. However, they may not be enough to explain the fact that the relative population level of adults to pupae was distinctly higher in 1974 than in preceding three years. Efficiency in collecting adults may have been more or less improved in this year through the change of collectors and/or environment in and around the pigsties.

Nakata (1956) postulated that the species passes five or six generations in a year in Kyoto, Japan and each generation has a more or less recognizable peak. Also, in the present data, about five peaks were recognized in the pupal prevalence except for 1974. However, it is difficult to consider all the peaks to represent more or less discrete generations. In every year, the feeding peak of overwintered females was observed in early or middle April. In view of the developmental period (Table 8), pupae of the first generation are expected to occur from late April to early May, which agrees with the date of the yearly first finding of adult males (Wada *et al.*, 1975). The appearance time of second generation pupae is expected to be late May or early June. These first two generations were more or less discrete insofar as pupae were concerned. However, the short developmental period, oviposition repeated over a considerable duration, heterogeneity of larval habitats, and immigration of adult females from other areas with different conditions must make it quite difficult that succeeding generations are kept distinct each other. The thermal constant required for the completion of one generation (K) and the threshold temperature for the development (t_0) of *tritaeniorhynchus* are considered to be less than 250 day-degrees and about 10°C, respectively (see Section 5). It means that seven or more generations are possible in the climatic condition of Nagasaki. However, only five generations may be realized if every generation meets bad conditions. The age structure of immature stages (Table 9) also support the above view. In 1972 and 1973, several peaks were found in the seasonal prevalence of first instar larvae, but it was difficult to ragard them as distinct generations judging from the developmental period. Most probably, they were produced by external factors which influence the size of egg populations and/or the survival rate of larvae. A good example was found in 1971 when, as mentioned earlier, temporary discontinuity of first instar larvae was brought by the heavy rain in late July. Further, it is difficult to correlate each peak of first instar larvae with the pupal one. In conclusion, the number of generations per year is variable and midsummer and autumn populations are considered to be the mixture of different generations.

Diapause in adult females of *tritaeniorhynchus* is induced by the short photoperiod in autumn(Kawai,1969). He demonstrated that most females which emerge after middle September are gonoinactive in Nagasaki. Therefore, it is a little strange that no pupae were discovered in September except for 1974 in spite of a considerable number of overwintered females. Probably, this phenomenon was due to the active flight of females before hibernation and the resultant concentration of females in particular areas. Overwintered females of the species are known to be collected in limited areas (Yamamoto and Manako, 1968; Wada *et al.*, 1973).

Lastly, the pupal number will be compared with the adult one. Except for the unusual year of 1974, the maximum numbers of median-aged pupae were about 800,000, 100,000 and 1,100,000 in respective years from 1971 to 1973. On the other hand, the maximum numbers of adult females/man/10 minutes/pigsty were 170, 35 and 90 in the corresponding years. This comparison may give an impression that the latter are too small, but this first impression is not necessarily quite justifiable. Provided that 1,000,000 adults emerge per day and a half of them are females, 500,000 females emerge per day. Supposing further that one fifth of emerged females take blood from pigs, it follows that 100,000 females take blood from pigs on one night. On the other hand, the actual number of females was at most 200 per man per 10 minutes per pigsty. This collection means that mosquitoes were collected by an aspirator at the rate of one female per three seconds. In the condition of our pigsties, the collection at this high rate was possible only when mosquitoes were very abundant and no efforts were necessary to find them. In this circumstance, a ten-minutes collection allowed us to cover only a small part of the place where mosquitoes rested. Further, results of all-night observation (Ogata *et al.*, 1968; Wada*, 1969; Wada *et al.*, 1970; Sonoda, 1971 and so on) show that the flight of *tritaeniorhynchus* to baits continues throughout the night, although the largest peak usually follows the sunset. Therefore, it is highly probable that 200 females are equivalent to only a very small part of the total mosquitoes attracted to each pigsty on the night. If we assume that 200 females are equivalent to one hundredth of the latter, mosquitoes per pigsty per night count 20,000, and the grand total at five pigsties in the study area does 100,000 which is equal to one fifth of the pupal number. Although this calculation is based on various hypothetical values, it may show that the number of females collected at pigsties was not unreasonably small as compared with the pupal number. However, overestimation of the pupal number may also be involved. The reason is as follows. The procedure to calculate the total number of larvae and pupae in the study area (see Section 6.1.1) was based on the assumption that samples are taken at random without considering intra-ricefield distribution of the aquatic stages. However, this assumption is not necessarily satisfied in the field. When we study mosquito populations in large ground pools such as rice fields, we tend to take a dip avoiding the site where the occurrence of mosquitoes is not expected at all. For instance, we do not prefer to take a dip at the windward, because we know that larvae are more abundant at the leeward when it is windy. Nevertheless, in our calculation, all the water-logged area was regarded to be equally suitable for the breeding of *tritaeniorhynchus*, thus overestimation may have been inevitable. Fortunately, however, this type of overestimation, if any, is considered to have no correlations with the developmental stage, therefore relative relationships among respective stages would not be affected by it.

6.3 The Survival Rate of Larvae

As seen already (see Section 6.2), one feature of *tritaeniorhynchus* populations is the overlapping of generations. Another important feature is the unstableness of age structure, which is clearly seen from Table 9. The age structure varies drastically from time to time, thus the one observed on each day is considered to represent a section of the age structure which is constantly varying following the fluctuation of egg numbers and survival rates. This

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* Yoshitake Wada. Be cautious not to confuse Yoshito Wada and Yoshitake Wada when literature is consulted.

two features of *tritaeniorhynchus* populations make it quite difficult to analyse the population, since most methods for population analyses have been developed for populations with discrete generations or stable age structure.

The census was done with a regular interval of one week as a rule, therefore the overall age structure for each year is considered to be useful to know the general level of survival rates in immature stages. Here the survival rate means the ratio of a later stage to the first instar larva based on the numbers at the median age of respective stages. The results are presented in Table 10. The yearly total pupation rate did not exceed 0.1 in every case. Yearly averages including all the rice fields ranged from the minimum 0.0287 in 1974 to the maximum 0.0602 in 1973, the average for four years being 0.0426. In other words, about 0.95 of median-aged first instar larvae died before reaching the median age of pupae, which means that the emergence rate (the ratio of emerged adults to hatched larvae) was still lower. Therefore, it can be said that the mortality in aquatic stages is generally very large in this area. Since the area is considered to have normal conditions for the breeding of *tritaeniorhynchus* in Nagasaki, the above figures probably show the general level of survival (or mortality) rates in immature stages at least in Nagasaki. Also, it is worth adding that pupation rates were higher in cultivated rice fields than in uncultivated ones except for 1974.

Survivorship curves (Fig. 16) may be helpful to examine the mode of death in aquatic stages. Lengths of respective stages are drawn roughly in proportion to actual lengths in summer, so they are not only age-specific survivorship curves but also a kind of time-specific ones. There were two periods when survival rates were variable from year to year or according to the type of rice fields. One is the period from the first instar to the second instar, the other is that from the fourth instar to the pupa. In 1971, for instance, about 0.9 of first instar larvae grew into the second instar in cultivated fields, while the rate was only 0.25 in uncultivated ones. In the period from the second instar to the fourth, the variation in mortality was relatively small, so the reversal of ranking in survival rates was rather uncommon then. This indicates the following tendency: the more the second instar larva, the more the fourth instar larva, if the initial number is identical. In fact, lower survival rates of fourth instar larvae in uncultivated fields were due, without exception, to large mortality in this early period. Survival rates were variable again in the period from the fourth instar to the pupa,

Table 10. Yearly total survival rates of immature stages of *Culex tritaeniorhynchus* in the study area

Year	Survival rate*									
	Cultivated field					Uncultivated field				
	L1	L2	L3	L4	Pupa	L1	L2	L3	L4	Pupa
1971	1.0000	0.9054	0.8400	0.3702	0.0402	1.0000	0.2406	0.1667	0.0897	0.0010
1972	1.0000	0.6406	0.7001	0.6085	0.0495	1.0000	0.2598	0.2670	0.1353	0.0015
1973	1.0000	0.8202	0.6926	0.2515	0.0645	1.0000	0.5288	0.5740	0.1897	0.0466
1974	1.0000	1.7248	1.0414	0.6461	0.0069	1.0000	0.4814	0.5541	0.1588	0.0980
Mean					0.0403					0.0368

*Calculated from total numbers in Table 9.

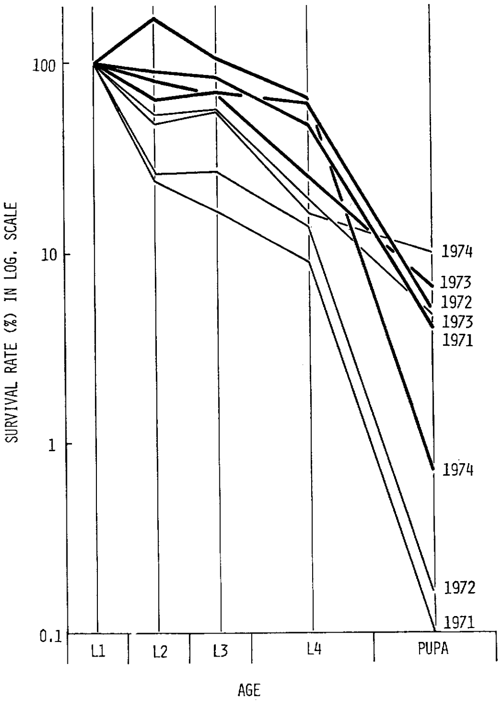

Fig. 16. Age-specific survivorship curves of *Culex tritaeniorhychus* larvae and pupae in the study area. Thick line : cultivated field. Thin line: uncultivated field.

when the ranking was rearranged.

Probably, the mortality in young larvae occurs in a strongly all-or-none manner. In rice fields where physical, chemical and/or biological conditions are quite unsuitable for larvae, almost all the larvae die out in a short period after hatch. In other words, the survival rate in this period is expected to be inversely proportional to the rate of rice fields which accept gravid females but do not allow larvae to survive. If this is the case, most second instar larvae would appear in more or less suitable rice fields, which may explain well the relatively small variation in survival rates in the succeeding larval period. The considerable variation in survival rates from the fourth instar to the pupa, on the other hand, is probably due to the fact that pupation is a critical step in a physiological sense when the difference in conditions during larval development may be expressed collectively. For instance, ill effects of food shortage may be expressed most severely in this period of the metamorphosis.

Pupation rates (S_P) and daily survival rates (s_P) at various seasons were obtained as follows. Firstly, the mean of daily mean air temperatures was calculated for 15 (April, May and October), 10 (June and September) and 7 (July and August) days after each census. Next, the duration for median-aged first instar larvae to reach the middle age of pupae (D_L') under this temperature was calculated as follows.

$$D_L' = D_{L1}/2 + D_{L2} + D_{L3} + D_{L4} + D_P/2 \quad \cdots\cdots \quad (21)$$

This gives the expected date when median-aged pupae were produced from median-aged first instar larvae found on each census day. Conveniently, the estimated duration was just 7 days or its approximations in summer, which means that sampling was done just on the day when pupae were produced from first instar larvae observed on the preceding census or its near date. Interpolation was applied to the estimation of the pupal number on the day when the census had not been done. Thus, obtained were pupation rates (S_P), from which daily survival rates (s_P) were calculated based on the following relation.

$$s_P{}^{D_L{}'}=S_P \cdots\cdots\cdots \quad (22)$$

When S_P was zero, it was assumed to be 0.0001, for convenience sake, to calculate s_P. In this case, the obtained value of s_P indicates that the actual rate did not exceed the calculated one.

The results are presented in Table 11. In the early or late season, pupation rates were seldom calculable (the number of first instar larvae was smaller than the corresponding pupal number), which means that estimated numbers of larvae and/or pupae were unreliable because of low density. As reported previously (Wada *et al.*, 1971b), the precision level decreases with the lowering density when a fixed number of rice fields are examined. Therefore, were set up density levels above which the estimated number of first instar larvae can be regarded as tolerable for further analyses. They are 10 larvae per m^2 (0.05 per dip) for cultivated fields and 200 per m^2 (1.08 per dip) for uncultivated ones. In Table 11, cases meeting this qualifications are indicated by asterisks. The number of larvae in Table 11 is not necessarily proportional to the density per m^2, since the former is influenced by the area of the water surface. This is the reason why some days lack the asterisk in spite of considerably large populations and *vice versa*. Insofar as days with asterisks are concerned, the reversal of numbers (pupae are more numerous than corresponding first instar larvae) did not occur except for only one case (first instar larvae found on May 31 in 1973).

In cultivated fields, very high pupation rates were observed for first instar larvae which appeared in early July shortly after transplanting. Estimated pupation rates reached 0.4 and 0.3 in respective years of 1971 and 1973. The same tendency was found also in 1972, although the density of first instar larvae was lower than 10 per m^2. In other seasons, however, pupation rates were generally much lower, being usually less than 0.05. In uncultivated fields, on the other hand, high pupation rates were encountered in the later season, that is, late July in 1973 and early September in 1974. The above indicates a possible tendency of considerable importance: in cultivated fields, suitable conditions for *tritaeniorhynchus* larvae are produced immediately after transplanting rather exclusively, while they occur rather irregularly in uncultivated ones (This phenomenon will be discussed again in Section 6.6 from various aspects).

Also, daily survival rates fluctuated greatly, reaching about 0.9 at the maximum, but more frequently being about 0.6 or much less. It is worth noting that the fluctuation in daily survival rates is much amplified in pupation rates. The daily survival rates of 0.84 which had been observed for first instar larvae found on July 5 of 1973, for instance, resulted in a very high pupation rate over 0.3, while a fall of the former to 0.5 in late July of the same

Table 11. Pupation rates of *Culex tritaeniorhynchus* in the study area

Date		Cultivated field				Uncultivated field			
		No. (10^3)		Pupation rate	Daily survival rate	No. (10^3)		Pupation rate	Daily survival rate
L1	Pupa	L1	Pupa			L1	Pupa		
1971									
Apr. 15	May 1	0	13	∞		0	0	—	
22	6	0	66	∞		0	0	—	
30	14	0	118	∞		0	0	—	
May 4	17	0	59	∞		0	0	—	
14	26	0	0	—		0	0	—	
20	31	0	27	∞		0	0	—	
27	Jun. 6	0	27	∞		0	0	—	
Jun. 3	12	0	98	∞		0	0	—	
10	19	0	214	∞		0	0	—	
17	26	0	178	∞		0	0	—	
22	30	161	336	2.0870		0	0	—	
Jul. 1	Jul. 8	1450*	572	0.3945	0.8756	959**	0	0.0000	0.2683>
9	16	36122*	775	0.0215	0.5778	33	0	0.0000	
15	22	30460*	504	0.0165	0.5563	22**	0	0.0000	0.2683>
26	Aug. 1	0	92	∞		0	0	—	
31	7	5119*	192	0.0375	0.6250	0	0	—	
Aug. 9	16	439	28	0.0638		0	1	∞	
17	24	0	0	—		0	0.3	∞	
27	Sep. 3	0	0	—		0	0	—	
Sep. 3	11	0	0	—		0	0	—	
8	16	0	0	—		0	0	—	
16	24	70	0	0.0000		0	0	—	
22	Oct. 1	82	0	0.0000		0	0	—	
1972									
Apr. 13	Apr. 27	43	0	0.0000		0	0	—	
21	May 7	227	0	0.0000		0	0	—	
27	10	0	0	—		0	0	—	
May 4	16	0	0	—		0	0	—	
11	24	0	0	—		0	0	—	
18	30	49	44	0.8980		0	0	—	
25	Jun. 4	2	35	17.5000		0	0	—	
Jun. 1	11	191	19	0.0995		0	0	—	
8	17	248*	25	0.1008	0.7749	0	0	—	
15	24	526*	0	0.0000	0.3594>	0	0	—	
23	Jul. 1	512	18	0.0352		0	0	—	
29	6	0	63	∞		0	0	—	
Jul. 7	14	124	83	0.6694		0	0	—	
14	21	336	64	0.1905		0	0	—	
20	27	3260*	113	0.0347	0.6187	0	0.3	∞	
25	Aug. 1	0	19	∞		34**	1	0.0294	0.6042
Aug. 2	9	1848*	64	0.0346	0.6187	1173**	0.1	0.0001	0.2683
10	17	416	0	0.0000		2	0	0.0000	
17	24	208	0	0.0000		115	0	0.0000	
24	31	725*	0	0.0000	0.2683>	409	0	0.0000	
31	Sep. 7	0	0	—		0	0	—	
Sep. 1	14	1603*	0	0.0000	0.2683	82**	0	0.0000	0.2683>
14	23	0	0	—		0	1	∞	
21	Oct. 2	0	0	—		137	1	0.0073	
28	10	0	0	—		0	0	—	

*Mean density of first instar larvae was higher than 10 individuals per m^2 of the water surface.
**Mean density was higher than 200 per m^2.

year lowered the latter to about 0.01, only one thirtieth of the former case (see also Table 14).

The relation of initial density to pupation rates (Fig. 17) strongly suggests the occurrence of density-dependent increase in mortality in immature stages of *tritaeniorhynchus*. When initial density exceeded 1,000 individuals per m^2, high pupation rates were not observed.

Table 11. (Continued)

Date		Cultivated field				Uncultivated field			
		No. (10^3)		Pupation rate	Daily survival rate	No. (10^3)		Pupation rate	Daily survival rate
L1	Pupa	L1	Pupa			L1	Pupa		
1973									
Apr. 5	Apr. 23	8	0	0.0000		0	0	—	
19	May 2	0	0	—		0	68	∞	
26	9	0	0	—		0	15	∞	
May 4	17	0	0	—		0	0	—	
10	22	0	0	—		0	0	—	
17	28	0	35	∞		0	0	—	
24	Jun. 4	0	114	∞		0	0	—	
31	10	17*	87	5.1176	1.1773	0	0	—	
Jun. 7	16	0	18	∞		0	0	—	
14	23	0	64	∞		0	0	—	
21	29	123	157	1.2764		0	17	∞	
28	Jul. 5	0	687			0	116	∞	
Jul. 5	12	1477*	450	0.3047	0.8439	2681**	4	0.0015	0.3950
12	19	20963*	1125	0.0537	0.6585	3171**	1	0.0003	0.3139
19	26	13747*	131	0.0095	0.5140	1757**	304	0.1730	0.7783
25	Aug. 1	2318*	19	0.0082	0.5035	1878**	102	0.0543	0.6596
Aug. 2	9	967*	0	0.0000	0.2683>	297**	14	0.0471	0.6463
9	15	1285*	0	0.0000	0.2151>	3535**	4	0.0011	0.3213
17	24	115	0	0.0000		0	0	—	
23	30	1593*	0	0.0000	0.2683>	137**	0	0.0000	0.2683>
30	Sep. 7	0	0	—		108	0	0.0000	
Sep. 6	15	0	0	—		0	0	—	
14	23	76	0	0.0000		30	0	0.0000	
20	30	76	0	0.0000		0	0	—	
1974									
Apr. 18	May 4	0	0	—		0	0	—	
25	9	0	0	—		0	0	—	
May 2	14	0	0	—		0	0	—	
14	25	0	0	—		0	0	—	
29	Jun. 8	0	5	∞		0	0	—	
Jun. 5	16	0	7	∞		0	0	—	
13	23	14	0	0.0000		0	0	—	
20	30	412*	0	0.0000	0.3981>	0	0	—	
Jul. 4	Jul. 12	353	0	0.0000		1	0	0.0000	
11	19	93	0	0.0000		0	0	—	
18	26	0	0	—		1	0	0.0000	
25	Aug. 1	594	0	0.0000		0	0	—	
Aug. 1	8	104	0	0.0000		12	0	0.0000	
8	15	208	0	0.0000		1	0	0.0000	
20	27	0	0	—		0	26	∞	
29	Sep. 5	104	0	0.0000		36**	4	0.1111	0.7306
Sep. 5	13	0	0	—		85**	17	0.2024	0.8190
12	21	0	0	—		436**	0	0.0000	0.3594>

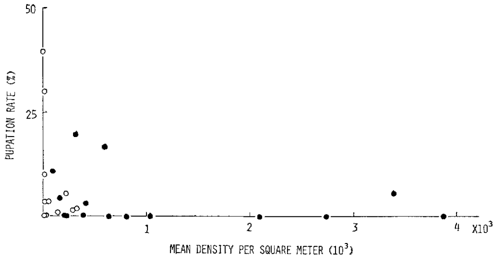

Fig. 17. Relation between the initial density of first instar larvae of *Culex tritaeniorhynchus* and pupation rates. Hollow circle : cultivated field. Solid circle: uncultivated field.

It is note worthy that such high density was encountered exclusively in uncultivated fields, which indicates that ill effects due to overcrowding tend to occur more seriously in uncultivated fields where the water-logged area is generally much smaller than in cultivated ones (see Section 3). Of course, it does not exclude the possibility that density-dependent mortality occurs in cultivated fields. Considering the great inter-ricefield variation in larval density (Wada *et al.*, 1971a), density sufficiently high to induce density-dependent mortality probably occurs in a part of rice fields even when the average density is low (see Section 6.6.18.1).

6.4 The Oviposition Rate of Adult Females

The oviposition rate (S_A) is defined here as follows for convenience sake.

$$S_A = \textit{No. of first instar larvae}/(\textit{No. of pupae} \times 0.5 \times 200) \quad \cdots\cdots\cdots\cdots\cdots\cdots (23)$$

where 0.5 is the rate of females and 200 is the mean number of viable eggs in an egg raft. If the population were closed and there were no emigration and immigration, the oviposition rate thus obtained would be regarded as an rough index proportional to the survival rate in the adult stage. Populations of *tritaeniorhynchus*, however, can never be regarded as closed in view of a great ability to fly of the species (see Section 6.6.17). Therefore, oviposition rates based on Equation (23) are apparent ones, that is, they result from both true oviposition rates and migration rates.

Yearly total oviposition rates were calculated following the similar procedure applied for the calculation of yearly total survival rates, the results of which are presented in Table 12. They ranged from the minimum 0.1662 in 1973 to the maximum 0.3485 in 1974, the mean being 0.2515. These values are much larger than the general level of pupation rates (see Table 10). The overall average oviposition rate 0.2515 means that females equivalent to about one fourth of those emerged in the study area laid eggs.

For further analyses, the relation between the pupal number and the number of corresponding first instar larvae was examined. In principle, the calculation procedure was the same as that adopted for the calculation of pupation rates, but a little modification was introduced. Day-to-day correspondence is not considered to give a reliable estimation of the oviposition rate, since the duration from emergence to oviposition is strongly influenced by various factors other than temperatures (see Section 5.4). Therefore, period-to-period correspondence was adopted. Here was taken a period of 10 days, for convenience sake. Firstly, the cumulative number of median-aged pupae was calculated for each period of 10 days. Next, the appearance

Table 12. Yearly total apparent oviposition rates of *Culex tritaeniorhynchus* in the study area

Year	Apparent oviposition rate*
1971	0.2522
1972	0.2389
1973	0.1662
1974	0.3485
Mean	0.2515

*Calculated from total numbers in Table 9.

duration of first instar larvae produced by these pupae was estimated based on the mean temperature for 20 (April and early May), 15 (middle and late May) and 10 (June-September) days after the first and last days of each 10-day period of the pupal appearance. Then, the cumulative number of median-aged first instar larvae was calculated for this duration. The oviposition rate was obtained from these cumulative numbers following Equation (23).

The results are presented in Table 13. Theoretically, there are no upper or lower limits for apparent oviposition rates. The infinite is probable, since a considerable number of immigrants may oviposit when the pupal density in the study area is so low that no pupae can not be detected by the census. Also, the emigration of most adults from the study area may reduce the apparent oviposition rate to zero. However, the infinite or zero in spring or autumn can rightly be attributed to the fact that the density was generally too low in these seasons to give reliable estimations of pupal and/or larval numbers (see Section 6.3). In summer when the population of immature stages was considerably large except for 1974, the following tendency was recognized: pupae which appeared in late June laid eggs at very high rates (at least apparently), but the rates were much lower in the succeeding and probably preceding seasons. In summer, it requires about 10 days for pupae to produce first instar larvae of the next generation, thus pupae which appear in late June are expected to lay eggs in early July. As mentioned repeatedly, the water-logged area is largest and most stable in this period immediately after transplanting (see Section 3). It is sure that this extension of suitable breeding places is the main factor responsible for high oviposition rates of females which appeared in late June as pupae. However, the rate itself presents a difficult problem.

The maximum rate was 0.8521 observed for pupae which appeared in late June, 1971. The oviposition rate of 0.85 in the midsummer is equivalent to the daily survival rate of 0.98 in a closed population or a population with an equal rate of immigration and emigration. Even the oviposition rate of 0.1 can be obtained through the daily survival rate as high as 0.8. Further, the above calculation of survival rates was based on the assumption that all the physiologically matured females take blood and lay eggs, therefore the actual survival rate is required to be still higher. The daily survival rate of adult females can also be estimated from the parous rate by the method proposed by Davidson (1954), if the duration of one gonotrophic cycle is known. Thus, we once obtained 0.24 as the estimation of the daily survival rate in summer. This value is considered to show the general level of daily survival rates in the summer population of *tritaeniorhynchus* in our country, in view of the mean parous rate and the mean duration of one gonotrophic cycle, both in summer: the former is generally in the range from 0.2 to 0.3 (Harada *et al.*, 1967; Buei *et al.*, 1968; Sasa *et al.*, 1968; Nishigaki, 1970 and so on) and the latter can rightly be regarded to be five days or its approximation. Even when the parous rate is as high as 0.3, the daily survival rate over 0.8 can not be expected. Therefore, survival rates obtained in this study are very high as compared with those obtained by Davidson's method.

This discrepancy can partly be attributed to the fact that a part of females lay eggs twice or even more, but its contribution is not very large. Provided that the population level is constant and all the living females lay eggs, the relation between the daily survival rate

Table 13. Apparent oviposition rates of *Culex tritaeniorhynchus* in the study area

Pupa		First instar larva		Apparent oviposition rate
Period	No. (10^3)*	Period	No. (10^3)*	
1971				
May 1–10	586	May 22–May 28	0	0.0000
11–20	835	May 29–Jun. 6	0	0.0000
21–31	88	Jun. 7–Jun. 14	0	0.0000
Jun. 1–10	398	Jun. 15–Jun. 23	1055	0.0265
11–20	2009	Jun. 24–Jul. 1	12280	0.0611
21–30	1584	Jul. 2–Jul. 8	134974	0.8521
Jul. 1–10	5026	Jul. 9–Jul. 19	327440	0.6515
11–20	7125	Jul. 20–Jul. 29	56020	0.0786
21–30	3167	Jul. 30–Aug. 9	31885	0.1007
Aug. 1–10	1624	Aug. 10–Aug. 20	1728	0.0106
11–20	598	Aug. 21–Aug. 29	0	0.0000
21–31	1	Aug. 30–Sep. 10	27	0.2700
Sep. 1–10	0	Sep. 11–Sep. 21	668	∞
11–20	0	Sep. 22–Oct. 2	323	∞
1972				
Apr. 20–30	0	May 14–May 21	282	∞
May 1–10	0	May 22–May 31	340	∞
11–20	0	May 31–Jun. 7	1591	∞
21–31	186	Jun. 8–Jun. 14	2569	0.1381
Jun. 1–10	262	Jun. 15–Jun. 23	4221	0.1611
11–20	253	Jun. 24–Jun. 2	1123	0.0444
21–30	21	Jul. 3–Jul. 10	1019	0.0444
Jul. 1–10	541	Jul. 11–Jul. 20	13412	0.2479
11–20	680	Jul. 21–Jul. 29	10486	0.1542
21–31	1043	Jul. 30–Aug. 9	21883	0.2098
Aug. 1–10	353	Aug. 10–Aug.19	3919	0.1110
11–20	221	Aug. 20–Aug 30	7812	0.3535
21–31	0	Aug. 31–Sep. 11	11008	∞
Sep. 1–10	0	Sep. 12–Sep. 22	1383	∞
11–20	0	Sep. 23–Oct. 7	294	∞
21–30	5	Oct. 8–Oct. 18	0	0.0000
Oct. 1–10	3	Oct. 19–Oct. 30	0	0.0000

*Cumulative No. which appeared during each period

of adults (s_A) and the oviposition rate (S_A) can be written as follows.

$$S_A=s_A^{10}\ (1+s_A^{5}+s_A^{5\times2}+s_A^{5\times3}+\cdots\cdots\cdots)\cdots\cdots\cdots\cdots(24)$$

where 10 is the mean duration from emergence to the first oviposition and 5 is that of one gonotrophic cycle, both in summer. By neglecting females laying eggs more than seven times, for convenience sake, we can get 0.9 for a rough estimation of s_A when S_A is 0.85 which is the maximum oviposition rate obtained in this study. Apparently, this value of s_A is still much higher than those calculated from the parous rate. Further, the daily survival rate of

Table 13. (Continued)

Pupa		First instar larva		Apparent oviposition rate
Period	No. (10^3)*	Period	No. (10^3)*	
1973				
Apr. 21-30	115	May 10-May 19	0	0.0000
May 1-10	524	May 20-May 28	25	0.0005
11-20	0	May 29-Jun. 5	93	∞
21-30	217	Jun. 7-Jun. 16	0	0.0000
Jun. 1-10	1125	Jun. 17-Jun. 23	501	0.0045
11-20	318	Jun. 24-Jul. 1	3809	0.1198
21-30	976	Jul. 2-Jul. 10	71534	0.7329
Jul. 1-10	6226	Jul. 11-Jul. 19	167113	0.2684
11-20	7893	Jul. 20-Jul. 29	66564	0.0843
21-31	5328	Jul. 30-Aug. 9	30321	0.0569
Aug. 1-10	462	Aug. 10-Aug. 18	17772	0.3847
11-20	39	Aug. 19-Aug. 29	11473	2.9418
21-31	0	Aug. 30-Sep. 10	513	∞
Sep. 1-10	0	Sep. 11-Sep. 23	1044	∞
11-20	0	Sep. 24-Oct. 4	66	∞
1974				
May 21-31	0	Jun. 7-Jun. 16	440	∞
Jun. 1-10	24	Jun. 17-Jun. 24	2922	1.2175
11-20	74	Jun. 25-Jul. 3	3384	0.4573
21-30	0	Jul. 4-Jul. 10	1694	∞
Jul. 1-10	0	Jul. 11-Jul. 20	632	∞
11-20	0	Jul. 21-Jul. 30	4070	∞
21-31	0	Jul. 31-Aug. 9	1681	∞
Aug. 1-10	0	Aug. 10-Aug. 18	941	∞
11-20	0	Aug. 19-Aug. 29	722	∞
21-31	208	Aug. 30-Sep. 10	1941	0.0933
Sep. 1-10	119	Sep. 12-Sep. 22	1744	0.1466
11-20	103	Sep. 23-Oct. 4	0	0.0000

0.9 means that more than 0.25 of emerged females lay eggs thrice or more. This is quite inconsistent with the fact that we rarely found females with more than three dilatations in the field (Harada *et al.*, 1968 ; Buei *et al.*, 1968 and our observation). Similarly, s_A is about 0.77 when S_A is 0.1. This value of s_A is nearly equal to highest ones expected from the general level of parous rates. Thus we can not but assume that immigration of gravid females into the study area occurred frequently and that not rarely in considerable extents. This assumption does not necessarily conflict with data on parous rates, since the fluctuation in parous rates is generally very large, 0.6 or still higher rates being observed for females collected on some days. This tendency is found in all the literature cited above in relation to the parous rate of *tritaeniorhynchus*. This may be due partly to the sampling error, but some samples may represent true age composition at the time and place when and where the collection was made. The parous rate 0.6 gives the daily survival rate of 0.9 which is an unlikely high rate as mentioned above. One explanation for these high parous rates is aging of populations following the decline or the stop of emergence. Increasing parous rates in autumn can surely be attributed to this. Another possible explanation is mass immigration of gravid females and their flight to near baits after oviposition. It seems to be sure that migration is a very important factor responsible for the great fluctuation in parous rates (age structure) of *tritaeniorhynchus*. In the summer of 1974 when the immature population was extremely small in the study area, the apparent oviposition rate was at the infinite almost constantly throughout the year, which can also be explained well by the supposition that there was constant immigration of gravid females being more numerous in number than those emerged in the study area.

The invasion of many gravid females into the study area is a likely hypothesis, since two requirements for its realization were probable. They are the presence of both the area holding large populations than in the study area and the condition helpful to immigration of gravid females into the study area. The first necessity is considered to have been satisfied by the presence of the rice field area extending towards the north from the study area (Fig. 1). It may be worth adding that a center for active breeding of *tritaeniorhynchus* in the valley was observed to move from the south (lower part) to the north (higher part) with the progress of seasons from spring to summer (Mogi and Wada, 1973). Also, the second necessity was probably satisfied, since the wind usually blew from north to south at night (mountain wind) in the valley. This wind may have helped mosquitoes to fly southwards. Although direct evidence is quite lacking at present, it is thought that immigration of gravid females was a possible and that main factor responsible for the appearance of first instar larvae more numerous than expected from the pupal number in the study area. It may be worth remembering that a considerable number of *Aedes vexans nipponii* invaded the study area constantly throughout the mosquito breeding season (see Section 4).

The relation of apparent oviposition rates to pupal numbers is shown in Fig. 18. There was found no clear tendency indicating the occurrence of density-dependent processes. However, it does not necessarily mean the true lack of density-dependent processes in the adult stage, because migration of adults may have been as extensive as it concealed density-dependent phenomena. Very or considerably high apparent oviposition rates observed at high

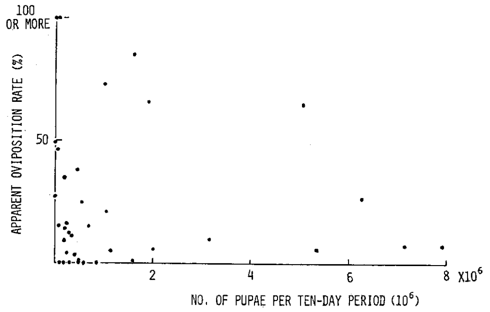

Fig. 18. Relation between the pupal number and the apparent oviposition rate in *Culex tritaeniorhynchus*. The infinite is included in 100 or more %.

pupal density may have been due to the invasion of a considerable number of gravid females into the study area.

6.5 Synthesis

Now, the process of the summer growth of *tritaeniorhynchus* populations can be explained as follows. The great increase of the water-logged area by transplanting results in a very high oviposition rate of females emerging in late June. Thus, the increase of the water-logged area is accompanied by the increased number of eggs per unit area. The larval density is increased further by very high survival rates in early July. Thus, the yearly peak of adults in the midsummer (Yamada's peak) is produced. The overall mean of pupation rates and that of apparent oviposition rates were 0.0426 and 0.2515, respectively (see Sections 6.4, 6.5), from which the following consideration can be derived. Provided that one gravid female lays 200 viable eggs, 8 adults emerge from them on an average. The sex ratio can rightly be regarded to be 1 : 1, so 4 females emerge from one gravid female. Females equivalent to about one fourth of emerged ones lay eggs, therefore one gravid female produces just one gravid female of the next generation. In this condition, the population is expected neither increase nor decrease, keeping nearly the same level. In other words, the population of *tritaeniorhynchus* in the study area can be regarded to have been in equilibrium insofar as the years from 1971 to 1974 are concerned.

It must be stressed, however, that this equilibrium could be attained by including extremely high rates of both pupation and oviposition in July, the period immediately after transplanting. Without this period of rapid increase in rice fields, the population level of *tritaeniorhynchus* would have been greatly lowered. Further, it must be remembered that this high oviposition rate would not have been attained without immigration of a considerable number of gravid females from the northern area. It means that in the northern area the reproduction rate was reduced by emigration of gravid females. Thus, migration of adults is considered to have played a very important role to keep the whole population of *tritaeniorhynchus* in the valley including the study area at a certain level of equilibrium (see also Section 6. 6.17).

6.6 Factors Influencing the Survival and Reproduction of *Culex tritaeniorhynchus* in the Study Area

In this section, there will be examined various factors which influence or may influence the population of *tritaeniorhynchus* in the study area. The discussion is based mainly on the essence of our observations but partly on literature. A part of factors were mentioned in the earlier sections. They will be listed here again for synthesis but explained as brief as possible to avoid repetition.

6.6.1 Temperature

Death of immature stages by the direct effect of extremely low or high temperatures is unlikely, at least in the usual breeding season of *tritaeniorhynchus* in Nagasaki. Immature stages were often reared in outdoor insectaries or in rice fields (a part of the results were presented in Tables 5, 6 and 7), but no indications of death by the direct effect of temperatures were observed. In spring, the daily minimum water temperatures were frequently much lower than the threshold temperature for development (the observed minimum was about 3°C), but larvae or pupae did not die. Freezing of water does not occur in the breeding season of *tritaeniorhynchus* in Nagasaki. As for high temperatures, Yoshida *et al.* (1974) observed that pupation rates begin to lower at the constant temperature of 35°C, being only 0.005 at 37.5°C. It was observed, however, that the maximum temperature near 40°C did not have bad effects on survival and development of *tritaeniorhynchus* in the field or semi-field conditions with variable temperatures.

Nothing is known to suggest the occurrence of adult death by the direct effect of temperatures in the breeding season. Also, death of overwintering females by low temperatures seems to be uncommon at least in Nagasaki. It was observed that the number of adult females put at the outdoor insectary in autumn decresed gradually during winter (Omori *et al.* 1965). Sudden decrease on the cold day was not observed. In north Japan the situation may be somewhat different from that in Nagasaki. In fact, Kato (1968), who studied *tritaeniorhynchus* populations in Miyagi, suggested a possible correlation between high temperatures of February (the coldest month) and the population level of *tritaeniorhynchus* in the succeeding summer.

Temperatures, however, influence seriously the survival rate by changing developmental periods (Table 8 and 14). For instance, at the air temperature of 18°C (in May), the larval duration is prolonged up to 2 weeks, while it can be shortened up to 6 days in the midsummer. Therefore, pupation rates in respective seasons differ greatly each other even if the daily survival rate is identical. Under the constant daily survival rate of 0.8, for instance, the survival rate on the sixth day is about 0.25, but it reduces to 0.04 after two weeks. It is sure that the increased pupation rate in early July (see Sections 6.3, 6.5) is attributable to the shortened developmental period by high temperatures, at least partly. As for additional favourable effects of high temperatures in this season, see Section 6.6.10. The above supports foregoing consideration that the summer temperature is a main factor responsible for the yearly change in the population size (see Section 6.2).

Table 14. Effects of developmental periods (D) on survival rates

Daily survival rate	Survival rate when D is							
	6	8	10	12	14	16	18	20
0.6	0.047	0.017	0.0060	0.0022	0.00078	0.00028	0.00010	0.000037
0.7	0.12	0.058	0.028	0.014	0.0068	0.0033	0.0016	0.00080
0.8	0.26	0.17	0.11	0.069	0.044	0.028	0.018	0.012
0.9	0.53	0.43	0.35	0.28	0.23	0.19	0.15	0.12

6.6.2 Humidity

Extreme dryness kills adult mosquitoes in a short time, especially when it acts in association with hotness. Also, *tritaeniorhynchus* is not an exception. It is quite difficult, however, to know how much natural death can be attributed to this factor.

6.6.3 Wind

The wind is undoubtedly a most important factor to control the amount and direction of adult dispersal. One aspect of its importance in the population dynamics of *tritaeniorhynchus* in the study area was mentioned already (see Sections 6.4, 6.5).

6.6.4 Precipitation

Direct death of adults by rainfalls can occur when large drops of rain strike mosquitoes, but this accident appears to be unimportant at least in the study area with enough suitable shelters (see Section 6.6.5). More females than had been expected was often collected at pigsties or by dry ice traps on a fine or cloudy night immediately after rainy days when the rain had been sufficiently heavy to prevent normal flight activity of mosquitoes. This gave us an impression that mosquitoes capable of taking blood had been accumulated during rainy days.

The amount and mode of precipitation influence immature populations both directly and indirectly (see Section 6.2). A remarkable example to show the direct effect of heavy rains was reported by Sakakibara (1965). He observed an outbreak of rice field breeders including *tritaeniorhynchus* due to the accumulation of larvae in a dam following a flood in rice field areas along upper streams. The precipitation in summer is considered to be a most responsible factor for the yearly change in the population size of *tritaeniorhynchus* in summer (see Section 6.2).

6.6.5 Shelters

Adult mosquitoes with a nocturnal habit rest in the daytime. Various devices for sampling resting populations were well reviewed by Service (1976). As for *tritaeniorhynchus* in Japan, Wada* (1970) collected many resting adults in the rice field area in Okayama. He collected mosquitoes in rice fields, vegetable fields and weed bushes by covering the area of 1.5 m^2 with mosquito nets, and found that the species prefers to stay under dense flat leaves near the ground, for instance, under leaves of sweet potatoes or strawberries. The collection of resting mosquitoes was tried in the study area by sweeping at bushes or rice fields (other crops were scarce in this area), but mosquitoes were rarely collected except for weed bushes by pigsties. It is considered that good shelters are readily accessible to *tritaeniorhynchus* in this terraced rice field area, since there are many small spaces in stone walls besides bushes arround the rice field area. Death due to the failure to find suitable shelters is unlikely.

6.6.6 Water currents

Importance of water currents on dispersal of immature stages was mentioned earlier in relation to rainfalls (see Sections 6.2, 6.6.4). Water currents may also influence immature populations indirectly through their influence on the water temperature and the amount of larval food. In all respects, stagnant water is best for the breeding of *tritaeniorhynchus*. A

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*Yoshitake Wada

good example is a nursery bed where water is kept stagnant to keep heat for rice plants of tropical origin. Water currents were generally small in fallow or uncultivated fields, but highly variable in cultivated fields.

6.6.7 Area of breeding places

Importance of the area of breeding places in the population dynamics of *tritaeniorhychus* can not be too stressed. It was already seen that the extension of the breeding area following transplanting leads to very high oviposition rates (see Sections 6.4, 6.5), which eventually leads to the midsummer peak of the species population. This fact suggests that it is not very easy in other circumstances for gravid females to find suitable places for laying eggs. Also, the survival of larvae is strongly influenced by the change in the area of breeding places. The effect of drying up is most severe, because it kills all the aquatic stages completely, although no drastic drop by artificial drainage was observed for the *tritaeniorhynchus* population in the study area where co-operative drainage was not done (see Section 3). It is sure that the mode of water management is a main factor to determine both the level and seasonal distribution of *tritaeniorhynchus* populations.

6.6.8 Food

The larva of *tritaeniorhynchus* is a filter feeder which consumes every small or fragile matter capable of being caught by its mouthbrushes (Mogi, 1978a). According to literature (Hinman, 1930; Laird, 1956 and so on), the main food of filter feeders in the field is small fragments of organic matter and micro-organisms, the amount of which is considered to fluctuate constantly under the interaction of water temperatures, water currents, fauna, flora, chemicals and so on. Direct death due to food shortage may be rather rare in rice fields except for small pools with extremely numerous larvae (see Section 6.6.18.1). However, delayed development by malnutrition seems to be usual. It was already indicated that the quantity and/or quality of food is frequently not very suitable in rice fields (see Section 5. 2). Also, Nakamura *et al.* (1971) obtained similar results. It was suggested from various observations that the mean level of larval food is low in fallow fields, high in both cultivated fields in early summer and nursery beds, and variable in both cultivated fields in late summer and uncultivated fields. This is considered to be total results of various factors (see Sections 6.6.1, 6.6.6, 6.6.10, 6.6.13).

Adults require water and sugar for survival. Water is easily accessible in rice field areas, but sugar may not be. Natural sources of sugar accessible to mosquitoes are nectar, fruits, sap, honey dew and plant dew. Harada et al. (1971) observed that the longevity of *tritaeniorhynchus* was more or less prolonged by supplying a flowering vine *Cyaratia japonica* (Family: Vitaceae), a common weed in bushes. However, flowers suitable for feeding of mosquitoes are not common in the study area at least in summer. It is unlikely that mosquitoes primarily live on nectar of flowers. They may live on plant dew which is secreted from water pores at night. This structure for water regulation is found on leaves of some plants including rice plants. If this is the case, death due to failure to find suitable sugar sources may be unimportant in rice field areas.

6.6.9 Hosts

For estimating the feeding rate of females, it is necessary to know both the number of emerged females and the number of females which have taken blood. It is so difficult to get these values in the field that no reliable data seem to be available at present for any mosquito species.

It is considered, however, that the number and distribution of hosts are very important factors to influence the reproduction rate of *tritaeniorhynchus*. Bases of this supposition are as follows. According to the observation by Gillies and Wilkes (1969, 1970) in Africa, the range where *tritaeniorhynchus* can detect stimuli from hosts is narrow. On the outside of this narrow range, the direction of flight is random in relation to the location of hosts. On the other hand, the distribution of hosts is not uniform but strongly biased, so it is highly probable that mosquitoes miss to enter this effective range. At present, the main blood source of *tritaeniorhynchus* in Japan is pigs and cows, therefore the population level of the species would greatly be influenced by the number, distribution and rearing conditions of these domestic animals.

6.6.10 Rice plants and weeds in rice fields

The rice plant and weeds are the main producer, on which the terrestrial animal community in the rice field area depends. Therefore, they influence the life of each members in the community through the fairly complicated web of life. Their importance is, however, not restricted to their role as the base of the food chain. They are dominant species which form the landscape in the rice field area, therefore their total effects on each species are probably too complicated to be described throughly. Here will only be referred to one aspect which seems to be essential to understand the population dynamics of *tritaeniorhynchus*. It is the thickness of plants or the degree of covering by plants.

In fallow fields, weeds are usually short but very dense (Figs. 5B and C). Therefore, generally speaking, early procedures in rice culture (cutting weeds, ploughing and irrigation which is done in a part of ploughed fields) are favourable for the breeding of *tritaeniorhynchus*, because they produce open ground pools being rich with infusion from weeds (Fig. 5D). In nursery beds, rice plants are set so densely that the part occupied by them is unsuitable for mosquito larvae. However, the open area surrounding the thicket of young rice plants is a very good habitat for mosquito larvae (Fig. 5E).

In rice fields, rice plants are arranged quite regularly on the grid, the distance between rice plants being about 20 cm in Nagasaki (Fig. 5F). Therefore, when rice plants are short, the water surface is quite open to direct sunlight, which produces very good conditions for *tritaeniorhynchus*. Firstly, gravid females can reach suitable places for laying eggs without meeting any obstacles. Secondly, the rise of water temperatures shortens the developmental period of the aquatic stages. Thirdly, accelerated is the multiplication of micro-organisms which are eaten by larvae. Fourthly, dead bodies of large organisms decompose speedily, which also increases larval food. Thus, early July following transplanting becomes the best season for breeding of *tritaeniorhynchus* together with the largest water-logged area at this time. Very high oviposition and pupation rates in this season can well be understood from these aspects. However, this good season does not last long, because rice plants grow very rapidly.

It was indicated earlier that peak density in uncultivated fields tends to occur in August or September. This phenomenon is attributable, at least partly, to short vegetation in a part of uncultivated fields, because short vegetation makes water open. Cutting of weeds in uncultivated wet fields often produces pools with the best condition. They are generally small but very rich with infusion from cut weeds and highly attractive to gravid females, especially in the late season when conditions of cultivated fields are growing worse day by day.

Both the species of duck weeds, *Spirodela polyrhiza* and *Lemna paucicosta* (Family: Lemnaceae), were few in rice fields immediately after transplanting, but many in the late season. In late Autumn or September, rice fields completely covered with duck weeds were not rare (Fig. 5H). Therefore, they strongly amplify bad effects produced by the growth of rice plants. Further, Makiya (1970) observed that they can be a good habitat for *Hydra* (see Section 6.6.15.2).

6.6.11 Chemicals of organic origin

Various water soluble chemicals can be produced or derived from plants, animals and bacteria in rice fields. They may be attractive or repellent to gravid females, and favourable or harmful (even lethal) to the aquatic stages. For instance, many egg rafts were often found in pools rich with infusion from weeds belonging to the family Gramineae. Also, it was found experimentally that infusion from some higher plants common in fallow fields, for instance a kind of butter cup *Ranunculus quelpaertensis* (Family: Ranunculaceae), is toxic to *tritaeniorhynchus* larvae, although it is quite unknown whether or not the toxic component actually reaches a concentration enough to kill mosquitoes. Similar positive or negative effects are produced possibly by aquatic lower plants or bacteria. Therefore, chemicals from weeds may influence mosquitoes also indirectly through their effects on the multiplication of these aquatic organisms. However, these aspects have scarcely been studied. At present, it can only be said that lethal chemicals of organic origin may be a factor responsible for an all-or-none type of death in young larvae (see Section 6.3) as selection of oviposition sites is not quite adaptive in *tritaeniorhynchus*. Females often lay eggs on the water unsuitable for development of larvae. The following is an extreme case to demonstrate it; when gravid females were allowed to select either tap water or water from fertilizer pits, most egg rafts were laid on the latter which was sufficiently strong to inhibit darkening of egg shells to say nothing of hatch.

Mucilaginous matter from seeds of weeds belonging to the family Cruciferae is known to stick mosquito larvae efficiently (Reeves and Garcia, 1969). Eshita *et al.* (1978) observed the same effect for some Japanese Cruciferae including common weeds in the rice field area. There was found a case in the study area that four larvae of *tritaeniorhynchus* were attached to mucilage secreted from one seed, but the role of this interesting phenomenon in the natural control of the species is quite obscure at present.

6.6.12 Light traps

Light traps were operated by farmers in a part of pigsties for health control of pigs. Efficiency of light traps to catch mosquitoes must strongly be influenced by structure of animal sheds. They catch mosquitoes very efficiently when they are operated in a small and closed space (Kamimura and Watanabe, 1973; Ikeuchi, 1976). Pigsties in the study area were rather small but quite open, therefore mosquitoes can fly in and out quite freely. Efficiency of light traps in this type of pigsties is unknown. It is worth stressing that light traps set in animal sheds catch many mosquitoes just after taking blood. For instance, Fujito *et al.* (1971) showed that about half females of *tritaeniorhynchus* in light trap collections at pigsties had blood on an average. At present, there are no reasons to regard mortality by light traps as insignificant. For further discussion on the effect of light traps, see Section 8.2.

6.6.13 Fertilizers

A large amount of fertilizers is applied to nursery beds and rice fields immediately before transplanting. It is uncertain whether or not they can be utilized by mosquito larvae directly, but they surely accelerate multiplication of micro-organisms, which increases larval food directly and/or indirectly. Therefore, application of a great amount of fertilizers may more or less contribute to raised pupation rates in early July.

6.6.14 Chemicals other than fertilizers

Here are included insecticides*, herbicides* and fungicides* applied to pests, weeds and diseases injurious to rice plants. No insecticides were applied in the study area with the purpose to control *tritaeniorhynchus*. Common insecticides used in the study area from 1971 to 1974 were NAC, BPMC, MPMC, PHC (these are carbamate), MEP, PAP (organophosphorus), chlorphenamidine (amidine) and cartap. Carbamate insecticides were predominant.

Reduction of adult numbers following the insecticide application to rice fields was observed in animal sheds or by dry ice traps (Kamimura and Katori, 1969; Self *et al.*, 1973 and so on). Kamimura and Matsuda (1972) observed that all the caged adults died out when they had been put in the rice field (no detailed explanation on microhabitats was given) during the aerial application of PAP. Observations by Self *et al.* (1973) are more instructive. They put caged adult mosquitoes under the dense foliage of rice plants, under that of bean plants, in houses and on the open ground during the aerial application of MEP, the resultant mortality being 1.00 for both *tritaeniorhynchus* and *Culex pipiens pallens* irrespective of the difference of microhabitats. Therefore, insecticides applied to rice fields can be a significant mortality factor, although the effect on adults in more concealed resting sites such as deep holes in stone walls is not proved yet.

Repellent effects of insecticides (on rice plants or in water) on gravid females may be worth examining. Very strong and long-lived effects can not be expected in view of reports

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*expressed in this paper by Japanese common names for active ingredients (see Appendix for corresponding English or chemical names).

that resurgence of the larvae quickly followed the stop of insecticide application (Ogata and Nakayama, 1963b; Nishigaki, 1970 and so on). However, short-lived repellent effects may be possible.

It was demonstrated by various investigators that insecticides applied to rice pests were lethal to larval or pupal mosquitoes in rice fields. An example observed in the course of this study is shown in Table 15, from which it is clearly seen that PHC for leafhoppers was very effective also to *tritaeniorhynchus* larvae, especially to the young stages. This forms a striking contrast to its inefficiency to *Anopheles sinensis* larvae at this dosage. This is only one example of the similar cases. It was frequently observed that *sinensis* larvae survived the application of insecticides by which *tritaeniorhynchus* larvae were killed almost completely.

Effects of insecticides on the aquatic stage, however, are considered not to be very persistent in usual circumstances. Numerous larvae were frequently found in rice fields within less than 10 days after the insecticide application. An example is shown in Table 16. No lethal effects were recognized on the tenth day after the treatment of PHC, although slight delay of development was recognized. However, there were no indications that the residue

Table 15. Effects of insecticides* on mosquito larvae. An example.

Species	Quadrat No.	Mean No. per dip just before the application (and 24 hours after the application)				
		L1	L2	L3	L4	Total
Culex tritaeniorhynchus	1	10.3(0.0)	14.5(0.1)	3.5(1.1)	0.8(0.3)	29.1(1.5)
	2	5.7(0.0)	10.4(0.0)	1.2(1.3)	0.0(0.1)	17.3(1.4)
	3	12.3(0.0)	10.5(0.0)	1.4(0.6)	0.4(0.0)	24.6(0.6)
	4	0.0(0.0)	0.5(0.0)	0.5(0.1)	0.2(0.0)	1.2(0.1)
Anopheles sinensis	1	0.9(0.9)	8.3(1.5)	0.0(6.6)	0.0(0.0)	9.2(9.0)
	2	0.0(0.1)	3.9(0.7)	0.0(3.2)	0.0(0.0)	3.9(4.0)
	3	3.5(1.1)	7.6(5.8)	0.3(8.2)	0.0(0.1)	11.4(15.2)
	4	0.3(0.0)	1.5(1.1)	0.0(1.8)	0.1(0.0)	1.9(2.9)

*1% PHC dust was applied at the dosage of 4 kg per 10 a to control leafhoppers.

Table 16. Quick recovery of conditions suitable for *Culex tritaeniorhynchus* larvae after insecticide application. An example.

Source of water	No. of replications	Mean No. of larvae*									
		After 24 hours					After 48 hours				
		L1	L2	L3	Dead	Total	L1	L2	L3	Dead	Total
Rice field treated with PHC 10 days before**	6	16.0	23.3	0.0	0.7	40.0	5.5	33.5	0.3	0.7	40.0
Rice field without treatment	4	7.7	32.1	0.0	0.2	40.0	1.2	35.8	2.7	0.3	40.0
Tap water***	1	6.0	34.0	0.0	0.0	40.0	5.0	24.0	11.0	0.0	40.0

* 40 first instar larvae were introduced into a dish for each replication.

** 1% PHC dust was applied at the dosage of 4 kg per 10 a to control leafhoppers.

***Food was added.

of the insecticide was directly responsible for this delay.

Representatives of herbicides were PCP, NIP, CNP, 2, 4PA, benthiocarb, and those of fungicides were MAF, DTAS, MAC (these three are organic arsenic), blastocidin S, kasugamycin (antibiotics). Their effects on *tritaeniorhynchus* have little been studied, but it is sure that a part of them are lethal to the species. Maeda *et al.* (1974) indicated experimentally that both NIP and CNP are lethal to *tritaeniorhynchus* larvae at the dosage much lower than expected in the field. In addition to direct effects, their simultaneous application with insecticides might produce synergism.

The rate of rice fields or nursery beds immediately after or just during the insecticide application on each census day is shown in Fig. 19, from which no distinct seasonal patterns are detectable. Insecticide application was done rather constantly throughout summer season. This confirms that no co-operative application was done in the study area. It is sure that the seasonal change in survival rates of larvae can not be correlated with the seasonal distribution of the insecticide application. In 1972, for instance, the number of cultivated fields was 180 and the standard frequency of insecticide applications after transplanting was four per year (see Section 3), therefore we can get 720 as an estimation for the total number of rice fields treated in this year. Provided that the duration for the application is 100 days, the expected number of rice fields treated per day is 7.2, which is equivalent to 0.04 of 180 cultivated fields, while actual rates in this year were largely in the range from 0.05 to 0.1. Higher actual values may have been due partly to erroneous inclusion of chemicals other than insecticides and partly to the extra application following the outbreak of pests. The daily application rate of 0.04 is not low, since eight days are required for hatched larvae to emerge even in the midsummer. This means that more than 0.3 of larvae which hatch on each day will be killed before emergence even if there are no other mortality factors. There is no doubt that insecticides are a very important mortality factor for aquatic stages of *tritaeniorhynchus* as well as for the adult. The effect of chemicals on the species population will be discussed further in Section 8.1.

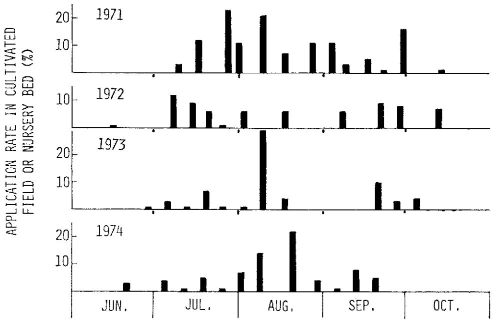

Fig. 19. Seasonal distribution of the insecticide application to rice pests, based on the observation on each census day.

6.6.15 Natural enemies

Families of natural enemies found in the study area are listed in Table 17. Additional notes are given below.

6.6.15.1 Enemies for eggs

Species to kill eggs appear to be a few insofar as we observed. Through series of experiments where egg rafts were released in rice fields, remarkable loss by predation was suggested only when many fishes were present. Other possible destroyers for eggs are small pond bugs belonging to the genus *Microvelia* (Vellidae), of which *M. douglasi* were very abundant on the water surface in summer.

6.6.15.2 Enemies for larvae and pupae

These aquatic stages are attacked by various predators. *Hydra japonica* (Hydridae) was found in the rice field with stagnant water. Sometimes, a considerable number of the species were found on dead leaves of rice plants hanging in water. Makiya (1970) observed experimentally that they prey on larvae of *Culex pipiens pallens*.

Naiads, nymphs of damselflies and dragonflies, are very efficient predators for mosquito larvae (Watanabe *et al.*, 1969 ; Nakamura *et al.*, and our observations). Genera included or possibly included were *Mortonagrion*, *Ceriagrion*, *Ishunura* (these three are Agrionidae), *Orthetrum*, *Sympetrum* and *Pantala* (Libellulidae), of which *Sympetrum* was predominant. The maximum density observed was 208 individuals per m^2 in a fallow field.

A water scorpion *Laccotrephes japonensis* (Nepidae) is an efficient predator (Watanabe *et al.*, 1969). This large predator, however, attacks other small predators, so its net effect may not necessarily be negative for *tritaeniorhynchus*. The density was low in rice fields studied.

Back swimmers of the genus *Notonecta* (Notonectidae) are very effective predators (Watanabe *et al.*, 1969 and our observations). The maximum density observed was 24 individuals per m^2 in a fallow field.

Three other heteropterous genera are inhabitants on the water surface. They are marsh treaders of the genus *Hydrometra* (Hydrometridae), small pond bugs of the genus *Microvelia* (Vellidae) and water striders of the genus *Gerris* (Gerridae), of which the species of *Microvelia* were very abundant in summer rice fields (see Section 6.6.15.1). All of them are voracious predators, and prey on organisms not only on the water surface but also just under it. In fact, Frick (1949) successfully colonized *Microvelia capitata* on anopheline larvae in Panama, and Hungerford (1920) found that aquatic stages of mosquitoes are the favorite food of *Hydrometra*. The larva of *Culex*, which usually touches the water surface only with the tip of the siphon, may be more resistant to these predators than the larva of *Anopheles* and the pupa of both *Culex* and *Anopheles*. In this sense, predators of this type might be more or less responsible for such phenomena as the increased mortality of *tritaeniorhynchus* around pupation (see Section 6.3) and the decreased number of *Anopheles sinensis* in the midsummer (see Section 4).

Only one larva of dobsonflies (Coridalidae) was found in our samples. The typical habitat of this species is running water. Apparently, it is a straggler in rice fields.

Table 17. Natural enemies for *Culex tritaeniorhynchus* observed in the study area

Stage attacked	Enemy			Type*	Stage attacking**
	Class	Order	Family		
Egg	Insecta	Hemiptera	Vellidae	Pr	L, A
Larva and Pupa	Hydrozoa	Hydroidea	Hydridae	Pr	L, A
	Insecta	Odonata	Agrionidae	Pr	L
			Libellulidae	Pr	L
		Hemiptera	Nepidae	Pr	L, A
			Notonectidae	Pr	L, A
			Hydrometridae	Pr	L, A
			Vellidae	Pr	L, A
			Gerridae	Pr	L, A
		Neuroptera	Corydalidae	Pr	L
		Coleoptera	Hydrophilidae	Pr	L
			Dytiscidae	Pr	L, A
		Diptera	Culicidae	Pr	L
	Osteichthyes	Cyprinida	Cyprinidae	Pr	L, A
			Cobitidae	Pr	L, A
		Cyprinodontida	Cyprinodontidae	Pr	L, A
	Phycomycetes	Blastocladiales	Coelomomycetaceae	Pa	
Adult	Arachnida	Araneae	Oecobiidae	Pr	L, A
			Theridiidae	Pr	L, A
			Mycryphantidae	Pr	L, A
			Argiopidae	Pr	L, A
			Tetragnathidae	Pr	L, A
			Agelenidae	Pr	L, A
			Lycosidae	Pr	L, A
	Insecta	Odonata	Argionidae	Pr	A
			Libellulidae	Pr	A
			Aeschnidae	Pr	A
		Hemiptera	Hydrometridae	Pr	L, A
			Vellidae	Pr	L, A
			Gerridae	Pr	L, A
		Coleoptera	Gyrinidae	Pr	A
	Amphibia	Anura	Ranidae	Pr	A
	Mammalia	Chiroptera	Vespertilionidae	Pr	L, A
			Rhinolophidae	Pr	L, A

* Pr : Predator. Pa : Parasite.
**L: Larva or young. A : Adult.

Most larvae of water scavenger beetles (Hydrophilidae) are known to be predators. In fact, Watanabe *et al.* (1969) observed that the larva of *Sternolophus rufipes* feeds on *tritaeniorhynchus* larvae. Also, Nakamura *et al.* (1969) found that the larva of *Hydrophilus affinis* preys on mosquito larvae. Several species were found in the study area, among which the species belonging to the genus *Berosus* was predominant in summer. However, this genus was reported to be an exceptional vegetarian (cited from Leech and Chandler, 1956).

Both the larva and adult of predacious water beetles (Dytiscidae) are active predators for larval and pupal mosquitoes. At least several species were recognized. The representative genera were *Hyphydrus*, *Laccophilus*, *Rhantus* and *Hydaticus*. Nakamura *et al.* (1969) observed that four species belonging to the above genera feed on mosquito larvae. The highest density observed was 23 individuals per m^2 in a cultivated field.

The predacious larva of *Culex halifaxii* was rarely found in rice fields (see Section 4). Its role in the natural control of *tritaeniorhynchus* may be negligible.

Three species of pradacious fishes were common in rice fields and irrigation ditches. They belong to *Carrasius* (Cyprinidae), *Misgurnus* (Cobitidae) and *Oryzias* (Cyprinodontidae), respectively. *Oryzias* is usually schooling up, so it could easily be recognized. The others were not easily observed, especially when water was turbid or covered with duck weeds, but their prevalence was evidenced by not a few dead bodies after the application of toxic chemicals. In fallow fields, fish density was generally low, because small, unstable and isolated pools are unsuitable for fishes. In this circumstances, they were denser in irrigation ditches connected with the river or irrigation ponds. In uncultivated fields, fish density was rather low throughout the year. After transplanting, rice fields are connected with ditches, which allows fishes to enter rice field filled up with water. Therefore, fish desity in rice fields tended to rise after transplanting. The highest density observed was 15 individuals of young *Carrasius* (about 5 cm or less in length) per m^2 in a cultivated field.

The fungus *Coelomomyces* is an only parasite which proved to kill immature *tritaeniorhynchus*. The species was described as new (Laird *et al.*, 1975). In view of general rareness of the species in this area, the sudden and short-term appearance of many parasitized larvae in some cultivated fields (July, 1973) is rather mysterious. No information on its life cycle is available at present (Mogi *et al.*, 1976).

To evaluate the mortality due to predators, two series of field experiments were conducted. In one series, eggs or first instar larvae were released in rice fields to examine the relation between the survival rate and predator density. In another series, observed were survival rates in enemy-free quadrats set in rice fields. Essence of the results is as follows. Firstly, there was a clear inverse correlation between the daily survival rate and the density of predators. When predator density was very high, no pupae were produced. Secondly, survival rates were increased remarkably in enemy-free quadrats, and pupation rates above 0.9 were not rare in July when the developmental period was very short.

The great contribution of aquatic predators to reducing mosquito populations has not necessarily been properly recognized. This is partly attributable to underestimates of predator density. In the usual sampling of mosquito larvae by dippers, predators are rarely collected in large numbers, which is apt to give us an impression that predator density is too low to control mosquitoes. However, this preoccupation must be removed, for which Tables 18 and 19 may be helpful. The data were obtained by the following procedures. A bottomless metal frame of 1 m^2 was pushed into the mud of the rice field quickly, and predator density in the frame was examined by dippers. Then the water was taken out from the frame, and the number of predators in the water or on the mud was counted.

Apparently, efficiency of the dipper in collecting predators is very low. For instance, the mean and maximum numbers of dragonfly nymphs (Libellulidae) per dip were less than one and only five, respectively, even when the absolute number per m^2 exceeded 150. The variation in the efficiency was very large. In an extreme case (Quadrat No. 2 in Table 18), only two naiads out of 208 were caught by 40 dips. On an average, one naiad per dip was equivalent to about 873 naiads per $1m^2$. This low efficiency may be rather natural, considering that naiads of Libellulidae are nocturnal bottom dwellers. Also, efficiency in dipping out fishes was very low. Ten individuals of *Carrasius* per m^2 were quite sufficient to eliminate

Tabie 18. Efficiency of the dipper in collecting predators for mosquito larvae in fallow fields

Predator		Quadrat No., Water depth(cm) and No. of dips (from the top to the bottom)								
		1	2	3	4	5	6	7	8	9
		5−6	3−5	2−5	5−10	2−6	2−10	2−4	2−4	3−5
		40	40	40	110	110	110	90	70	70
Agrionidae	A	11	6					13	4	1
	B	0	0					0	0	0
	A/C	*	*					*	*	*
Libellulidae	A	182	208	173	31	42	35	17	37	162
	B	16	2	31	5	10	7	10	7	14
	C	0.400	0.050	0.775	0.046	0.091	0.064	0.111	0.100	0.200
	D	3	1	5	1	1	1	1	2	1
	A/C	455	4160	223	674	462	547	153	370	810
Nepidae	A			1						
	B			0						
	A/C			*						
Notonectidae	A	16	24					22	4	9
	B	25	5					15	2	10
	C	0.625	0.125					0.167	0.029	0.143
	D	3	1					2	1	1
	A/C	26	192					132	138	63
Corydalidae	A							1		
	B							0		
	A/C							*		
Dytiscidae (adult)	A	6		5	5		9	4	1	7
	B	0		0	0		1	0	1	0
	C	0		0	0		0.009	0	0.014	0
	D	0		0	0		1	0	1	0
	A/C	*		*	*		1000	*	71	*
Dytiscidae (larva)	A		5							
	B		0							
	A/C		*							
Cobitidae	A			3			1	1		
	B			0			0	0		
	A/C			*			*	*		
Cyprinodontidae	A						1	1		
	B						1	0		
	C						0.011	0		
	D						1	0		
	A/C						91	*		

A : Absolute No. per m^2. B : Total No. dipped. C : Mean No. per dip. D : Maximum No. per dip. A/C : Conversion rate. * : A/C is incalculable because dipping efficiency and/or absolute density was too low.

Table 19. Efficiency of the dipper in collecting predators for mosquito larvae in cultivated fields

Predator		Quadrat No., Water depth(cm) and No. of dips (from the top to the bottom)									
		1 1−3 40	2 1−3 40	3 2−4 40	4 2−4 40	5 1−5 40	6 1−4 40	7 5−10 40	8 5−10 40	9 5−10 40	10 5−10 40
Agrionidae	A	3	22	3	9	11	43	4	2	15	4
	B	0	1	0	5	2	7	0	1	1	2
	C	0	0.025	0	0.125	0.050	0.175	0	0.025	0.025	0.050
	D	0	1	0	2	1	1	0	1	1	1
	A/C	0	880	0	72	220	246	0	80	600	80
Libellulidae	A	1			1		9	1	3		
	B	0			0		0	0	0		
	A/C	*			*		*	*	*		
Hydrophilidae	A	2	11	2	1	2		10	15	57	2
	B	0	0	0	0	0		9	2	3	0
	C	0	0	0	0	0		0.225	0.050	0.075	0
	D	0	0	0	0	0		2	1	1	0
	A/C	*	*	*	*	*		44	300	760	*
Dytiscidae (adult)	A		2	13	23		4	8	1	1	1
	B		0	0	0		1	1	0	0	0
	C		0	0	0		0.025	0.025	0	0	0
	D		0	0	0		1	1	0	0	0
	A/C		*	*	*		160	320	*	*	*
Cyprinidae	A	2	3	12	11	15					
	B	0	0	0	0	0					
	A/C	*	*	*	*	*					
Cobitidae	A							1			1
	B							0			0
	A/C							*			*
Cyprinodontidae	A	1									
	B	0									
	A/C	*									

A, B, C, D, A/C and * : See footnotes for Table 18.

mosquito larvae in a short time, but the dipper was useless to detect fishes at this density level. In Quadrats No. 3-5 (Table 19), all the released larvae disappeared in one or two days, which puzzled us very much until the problem was solved by the unexpected finding of many fishes in the drawn water.

The mortality due to predators is density-independent, however large it may be. All the predators listed are polyphagous, mosquitoes occupying a very small part of their menu. Further, predators require much longer periods for the development than mosquitoes, only one generation a year being not rare. Therefore, no positive and quick responses following the change in mosquito density can be expected. In fact, Nakamura *et al.* (1969) did not find any correlation between the density of predacious insects and that of *tritaeniorhynchus* larvae. Their experience is similar to ours. Increased pupation rates in early July may partly be attributed to the fact that predators can not follow the sudden appearance of a vast number of mosquito larvae.

In conclusion, predators are a very important factor responsible for high mortality rates in immature *tritaeniorhynchus*, but they can not suppress the rapid growth of mosquito populations under suitable conditions. Their effects are density-independent.

6.6.15.3 Enemies for adults

Spiders (Araneae) are considered to be very important predators for adult mosquitoes in view of their occurrence in every habitat where *tritaeniorhynchus* visits, their abundance and also their efficiency to catch mosquitoes. Species composition of spiders varies according to habitats, among which rice fields and animal sheds appear to be most important in relation to the population dynamics of *tritaeniorhynchus*. Here the latter include their neighbouring bushes, too. Seven main families predominant in these two habitats in Nagasaki are listed in Table 17.

The representative genera in rice fields are as follows: *Enoplognatha*, *Theridion* (these two are Theridiidae), *Oedothorax* (Mycryphantidae), *Neoscona*, *Singa* (Argiopidae), *Tetragnatta* (Tetragnathidae) and *Lycosa* (Lycosidae), of which *Lycosa* is a hunter without nets but the others are snarers which make nets. There are no direct field evidences to show their role in the natural control of *tritaeniorhynchus* populations, but various observations strongly suggest their importance. Some of them proved to prey on mosquitoes very efficiently in the laboratory. Also, efficiency of rice field spiders to kill mosquitoes was often ascertained by unwished experiments, that is, the elimination of caged mosquitoes in a short time by the accidental inclusion of spiders into the cage.

The spider fauna in cowsheds and their neighbouring bushes were studied by Ori (1975) in the Saga district adjacent to Nagasaki. According to him, representative genera are *Oecobius* (Oecobiidae), *Theridion* (Theridiidae), *Necosa* (Argiopidae), *Agelena* (Agelenidae), *Pardosa* (Lycosidae) and *Oxyopes* (Oxyopidae). The genera other than *Pardosa* are snarers. Examining preys on nets, Ori found that dipterous flies occupy a considerable part of their preys. Further, he found three species of mosquitoes including *tritaeniorhynchus* on the net of spiders. Possibly, a considerable number of *tritaeniorhynchus* are preyed by spiders in animal sheds and especially in the nearby bushes where both the spider density and the density of resting *tritaeniorhynchus* are high (see Section 6.6.5).

Spider density in cultivated fields is relatively low in the early season including the period immediately after transplanting, but increases gradually and reaches the yearly peak in late summer or autumn in southwest Japan (Kuno, 1968 ; Kawahara *et al.*, 1969 and so on). Therefore, the decreased oviposition rate of *tritaeniorhynchus* in late summer may have been due partly to the increased mortality by spiders. Seasonal prevalence of spider density in or near animal sheds may be somewhat different, because Ori (1975) found a tendency that the total number is rather larger in the early season. This possible difference in the seasonal distribution of spiders between two habitats suggests that the increase of spider density in cultivated fields is, to a certain extent, attributable to the invasion from the surrounding areas, following recovery or reproduction of suitable habitats for spiders by the growth of rice plants. In this sense, it is very likely that uncultivated fields serve as refuges for spiders, from which spiders are sent to cultivated fields with spider populations decreased or destroyed by transplanting or the insecticide application. If this is the case, the increased number of uncultivated fields may have been unfavourable for reproduction of mosquitoes.

Density-dependency is not expected insofar as mosquitoes are concerned, because mosquitoes occupy only a small part in the whole food of spiders. Kiritani, Kawahara *et al.*

(1972) found that leafhoppers are the main food of spiders in rice fields, and Ori (1975) observed that Chironomidae, Muscidae and Tipulidae are the main food of spiders in and around animal sheds. Also, one generation of spiders is much longer than that of mosquitoes. Therefore, no positive responses of spiders to increased mosquito density are expected.

Dragonflies and damselflies (adult Odonata) are active predators on flying small insects but they are diurnal except for a few species. Therefore, they may not be very important as predators for nocturnal mosquitoes such as *tritaeniorhynchus*.

All the predators belonging to Hemiptera are the surface inhabitants which feed on insects and other small organisms falling on the water surface (see Section 6.6.15.2).Therefore, adult mosquitoes on the water surface, especially those just emerging or having emerged, may readily be attacked by them, although no direct evidences are available at present. The same statement is applicable to whirligig beetles of the genus *Gyrinus* (Gyrinidae). However, rice fields are not a typical habitat of this beetle, therefore its density was not high.

Three species of frogs (Anura) belonging to the genus *Rana* were common in the study area. They are *nigromaculata*, *rugosa* and *limnocharis*. According to Okada (1966), they usually prey on animals much larger than mosquitoes. However, Miyagi (personal cmmunication) observed that they actively prey on mosquitoes when they were caged with mosquitoes. Therefore, they may be more efficient predators for mosquitoes than are expected.

Two species of insectivorous bats (Chiroptera) inhabit in the study area. One is *Pipistrellus abramus*, the other is *Rhinorophus ferrummequinum*. Some believe that insectivorous bats are very efficient natural enemies for mosquitoes, but this may need further confirmation, since they usually prey on much larger insects such as moths (Funakoshi & Uchida, 1975). In any case, they are so small in number that no practical importance is expected.

In conclusion, spiders are prominent among predators for adult mosquitoes, in their abundance and also in their efficiency to kill mosquitoes. Therefore, characteristics of adult mortality by predation may virtually be determined by spiders. As mentioned above, their predation on mosquitoes is characterized by the decrease in rice fields shortly after transplanting and the lack of density-dependency. The former may more or less help the rise of oviposition rate in early July by reducing the mortality during oviposition and emergence.

6.6.16 Insemination rates

It was observed by Harada *et al.* (1967) that nearly all the females collected at pigsties were inseminated. Also, they, as well as Kawai (1969), ascertained that females take blood irrespective of their sexual history. These two facts indicate that the insemination rate in the field must be very high.

6.6.17 Flight of adults

In earlier sections, migration of *tritaeniorhynchus* was often mentioned without presenting any evidence. In view of the importance of adult migration in the population dynamics of the species, it would be reasonable to refer to some important literature collectively.

Two types of evidences are available. One is the finding of the species at the place far apart from its normal breeding habitats (for instance, at ships, islets, the top of mountains, the center of big cities and so on) and the other is results of dispersal experiments with marked adults.

The best example may be the collection of the species on ships far apart from the land. Asahina (1970) reported the finding of *tritaeniorhynchus* on a ship being about 500 km from the nearest land. Also, Hayashi *et al.* (1978) found the species on a ship on the East China Sea. The species is not rarely found at islets lacking suitable conditions for establishment. Miyagi (1973a) found it at Danjo Islands, and it was found also at Chikuzen-Okinoshima Island (Mogi, 1977). Ito *et al.* (1975) reported that a large number of *tritaeniorhynchus* were constantly collected at the top of a mountain in summer. Occurrence of human JE cases caused by the biting of infected *tritaeniorhynchus* is well known not to be restricted to rice field areas where the vector breeds. They also occur sporadically at the center of big cities. These examples are only a part of typical cases reported. In mosquito surveys at various places, *tritaeniorhynchus* (larvae and adults) were frequently encountered at locations far apart from its normal breeding habitats such as rice field areas.

Dispersal experiments were done in Japan by two teams, at Kyoto (Uemoto et al., 1967; Maeda, 1968; Yamaguchi *et al.*, 1969) and at Nagasaki (Wada *et al.*, 1969). Both the results show that the normal flight range of this species is very large and at least 5 km can be traversed in one night by vigorous individuals meeting with favourable conditions. Even a case was found by the former team that a mountain of about 800 m in height was flown over in one day. Also, flight ability of *tritaeniorhynchus* females was preliminary examined with the tethered flight technique, and it was found that the continual fluttering for several hours is not rare.

All the evidences strongly indicate the great ability to fly of *tritaeniorhynchus*. Probably, the mosquito can move freely in the valley where this study was done if meteorological conditions are suitable. This gives the ground for the earlier speculation (see Sections 6.4, 6.5). Also, interchange among local populations is considered to be quite common (see Fig. 1).

6.6.18 Density effects

Density effects can be divided into three types, that is, exploitation of resourses such as food or space, conditioning of habitats and interference among individuals.

6.6.18.1 Density effects in larvae

As mentioned earlier, the pupation rate decreased with increasing larval density, being constantly lower than 0.05 above the average density of 1,000 individuals per m^2, and this suggested the presence of density-dependent mortality (see Section 6.3). In fact, Siddiqui *et al.* (1976) showed experimentally that the larval duration is prolonged, the pupation rate is lowered and the adult size is decreased when *tritaeniorhynchus* larvae are reared at high density. It may look strange that the lowest density in their experiments was 0.1 individual per cm^2 (just 1,000 individuals per 1 m^2), where they obtained a high pupation rate. Besides, water in our rice fields was usually deeper than 1 cm, while the water depth in their experiments was constantly 1 cm. However, this problem can easily be solved, considering the great inter-ricefield variation in larval density (see Section 6.3). Average density of 1,000 per m^2

means that there were a considerable number of rice fields where larval density was sufficiently high to cause severe density effects. In this sense, average density not necessarily indicates the real life of the species. This seems to be of fundamental importance to understand the population process of the species, and we already referred to it in an earlier paper (Mogi and Wada, 1973).

Further, ill effects of crowding may appear in the field at much lower density than in the laboratory. The reasons are as follows. Firstly, a sufficient amount of food is supplied in control series of laboratory experiments, while the quantity and/or quality of food in rice fields is usually below the best (see Section 5.2). Therefore, lowering of critical density for the appearance of food shortage may be rather natural in the field. Secondly, there exist many other mortality factors in the field, therefore, prolonged developmental periods result in much reduced pupation rates (see Table 14). This can not be expected in the laboratory without mortality other than malnutrition. Thirdly, cohabitation of various instars is normal in the field. Usually many larvae of advanced instars, frequently much more than first instar ones, are found with the latter. On the other hand, it is usual that laboratory experiments are started by introducing only first instar larvae into containers. This difference is important, because cohabitation of various age groups, especially of advanced ones, not only lowers critical density for the appearance of malnutrition but also produces necessary situations for occurrence of different types of density effects such as conditioning and interference. Ikeshoji and Mulla (1970) found that mosquito larvae accumulate in water the chemicals harmful to development and survival of succeeding generations (overcrowding factors), and Siddiqui et al. (1976) recognized the phenomenon in *tritaeniorhynchus* larvae. Mogi (1978a) found the severest type of interference in *tritaeniorhynchus* larvae, that is, death of young larvae due to predation by old ones. These phenomena, especially the former, are considered to play an important role in population regulation of mosquito species breeding in small but stable collections of water (container breeders), but to be much less important in ground pool breeders. It is considered that exploitation of food is the major aspect of density effects in larval *tritaeniorhynchus* in the field. Of course, overcrowding factors and/or cannibalism may play some roles in a part of very small pools with very high density.

6.6.18.2 Density effects in adults

Density-dependent processes were not so strongly suggested about adults, probably due to constantly occurring migration (see Section 6.4). Density effects in adults can be either of two origins. One is direct effects among adults themselves, and the other is indirect or delayed effects inherited from larvae.

Direct effects are rather unlikely, because adults are usually sparsely distributed. Exceptions are males in swarms and females on hosts. As for the former, no ill effects by the concentration are thinkable. As for the latter, Fujito *et al.* (1971) observed that the rate of engorged females decreased with the increasing total number of females collected by light traps at animal sheds. Also, the rate of females with only a small amount of blood was observed to increase with the increasing total number. They attributed these phenomena to interference among adult females, but the speculation seems not necessarily be quite acceptable.

They reported that the maximum number of females collected by light traps had exceeded 1,000 per pig per night and 3,000 per cow per night. These values, however, do not give information on actual density of mosquitoes on hosts. According to Wada* (1969) who did an all-night observation at a pigsty, the maximum number of *tritaeniorhynchus* females on an adult pig was about 800. He estimated that 50,000 females had taken blood from the pig in the night. This density level appears not to be incomparably lower than those at pigsties visited by Fujito's team. Provided that a half of the surface area of one pig is 1 m^2, 800 females per pig is equal to 8 females per 100 cm^2. As seen already for larvae, average density does not necessarily give precise information on real density experienced by mosquitoes, since distribution of females on hosts is not uniform but more or less concentrated at least in the usual level of density. Even considering this point, it is hesitated to regard the above density level high enough to reduce the feeding rate through interference among individuals, since mosquitoes, much more densely crowded on anesthetized or fastened small animals such as chickens or mice, are observed to take blood smoothly in the laboratory. Phenomena observed by Fujito *et al.* (1971) may be attributed to either irritation of hosts (a special type of conditioning?) or delayed density effects. The latter mean the change in physiological and/or behavioural characters of adult mosquitoes due to overcrowding of larvae. One fact which suggests the possibility is as follows; when flight ability of *tritaeniorhynchus* was preliminarily examined by the thethered flight technique (see Section 6.6.17), it was found a possible tendency that larval crowding increases fluttering hours in adult females.

6.6.19 Summary and general consideration on population dynamics of *Culex tritaeniorhynchus*

Conditions for the life of *tritaeniorhynchus* in Nagasaki greatly vary seasonally, not only following natural process but also following the process of rice culture. Considering this point, factors which proved or may prove to be important in relation to population dynamics of *tritaeniorhynchus* were summarized in Table 20. The division of rice fields in this table is, in principle, identical with that adopted by Ori *et al.* (1963). Density effects are excluded from the table, since they are not environmental factors but a kind of internal systems inherent to the population itself.

Based on Table 20 and all the preceding discussions, it can be concluded as follows: (1) Generally speaking, conditions favourable for reproduction of *tritaeniorhynchus* are scanty in the early season when rice fields are in fallow. (2) A combination of several favourable conditions is produced after transplanting, that is, in early July in the Nagasaki district. (3) The resultant increase in oviposition and pupation rates, in association with the largest and most stable water-logged area after transplanting, leads to the yearly peak population of adults in late July or early August (Yamada's peak). (4) This good period, however, does not last long, and conditions grow worse day by day. (5) Therefore, the population size in each year is dependent largely on conditions in July. (6) Major factors to influence reproduction of the species are considered to be temperature, precipitation, water management, hosts, natural enemies and insecticides including other toxic chemicals. (7) A combination of high

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Table 20. Summary of environmental factors which influence the life of *Culex tritaeniorhynchus* in the study area

Factor	Condition of rice fields				
	Fallow	Cultivated			Uncultivated
	April & May	Nursery bed June	Before earing Jul.–early Aug.	After earing Late Aug.–Sept.	June–Sept.
Air temperature (°C)	below 20	20–25	**25–30**	30–20	**
Water temperature (°C)	below 25	25–30	**30–35**	30–25	25–35
Precipitation	variable	variable	variable	variable	**
Wind	variable	variable	variable	variable	**
Water currents	**small**	**small**	variable	variable	**small**
Area of breeding places	small	small	**large**	**large**	small
Stability of breeding places	unstable	**stable**	**stable**	unstable	unstable
Mean level of larval food	low	**high**	**high**	variable	variable
Distribution of hosts	biased	biased	biased	biased	**
Height of rice plants/weeds	variable	**short**	**short**	tall	variable
Density of rice plants/weeds	dense	dense	**sparse**	dense	dense
Density of duck weeds	**sparse**	**sparse**	**sparse**	dense	variable
Light traps	**stopped**	operated	operated	operated	**
Fertilizers	no	**large**	**large**	small	no
Insecticides*	**no**	large	large	large	**no**
Enemy for eggs	?	?	?	?	?
Enemy for aquatic stages	numerous	numerous	numerous	numerous	variable
Enemy for adults	numerous	**small**	**small**	numerous	numerous

* Other toxic chemicals are included.
**Distinction between cultivated and uncultivated fields is unnecessary.
The best conditions are indicated by Gothic.

temperature and small precipitation is considered to be best for reproduction of the species. (8) All the six factors are density-independent in their manner of action. (9) Overcrowding in the larval stage is considered to be a main factor which regulates the species population. (10) Migration of adults is considered to occur constantly and that at considerable extents, population dynamics of the species being difficult to be understood without considering this factor. (11) Uncultivated fields are generally unattractive to the species, but suitable pools, which are occasionally produced, attract many gravid females, especially in late summer when the condition in cultivated fields is growing worse. (12) Therefore, uncultivated fields may play some roles in population regulation of the species, as well as their possible role as refuges for spiders which are the most important predator for the adult mosquito.

Among six major factors above mentioned, temperature and precipitation are meteorological, therefore they can not be controlled by present powers of man. On the other hand, water management, hosts (virtually pigs and cows in our country), natural enemies and chemicals are more or less under the control by man. Water management and the application of chemicals are a part of procedures for rice culture, pigs and cows are kept by farmers and the quality and quantity of natural enemies are also strongly influenced by rice culture procedures such as the application of chemicals and water management. Therefore, if we take a sufficiently short period of years during which the system of agriculture is kept unchanged, for instance the period from 1971 to 1974 in the study area, major factors responsible for the yearly fluctuation in the population size can be regarded as temperature and precipitation in summer, especially in July. On the other hand, when factors responsible for different population levels between the 1970's and the early 1960's are studied, it would be necessary to examine first the change in the rice culture system and other circumstances in rice field areas. Therefore, we can simplify and emphasize foregoing conclusions as follows.

(1) Factors responsible for the change in the average population level are what can be controlled or influenced by man, for instance, water management in rice fields, livestock, agricultural chemicals and natural enemies.

(2) Factors responsible for the yearly fluctuation in the population size are meteorological, especially temperature and precipitation in July being very important.

(3) The factor which regulates the population is intraspecific competition, probably in the larval stage.

Some may hesitate to accept the idea that the population of *tritaeniorhynchus* is being regulated through intraspecific competition in the larval stage, because *tritaeniorhynchus* density in respective rice fields is usually much lower than the maximum which can be kept there. They may say further that mortality due to overcrowding occupies only a small part of the total mortality in the area, however serious it may be in a part of rice fields. Such facts, however, do not conflict with the idea of population regulation by intraspecific competition. To make this point clearer, a simplified schema may be helpful (Fig. 20). Three situations are drawn to show the respective roles of density-independent mortality and density-dependent one in the determination of equilibrium density. Here, "mortality" is used in the broad sense including all the reduction in the reproduction rate, for convenience sake. If density-independent mortality reduces the number of progenies to the level lower than the equal density line between parents and progenies (Fig. 20A), the population will decrease, eventually becoming extinct if the tendency lasts. It should be noticed that density-dependent mortality may occur even in such a population towards extinction. If density-independent mortality leaves more progenies than the equal density line, the population will continue to increase until density-dependent mortality become sufficiently large to suppress the progeny density to the equal density line, thus the equilibrium will be attained (Fig. 20B). Of course, the level of equilibrium is strongly influenced by the extent of density-independent mortality. The less the density-independent mortality, the higher the equilibrium density. When density-independent mortality is very large, the population will be regulated at a very low level by density-dependent mortality which occupies only a small part of total mortality. In this circumstance, density effects working at a very small part of local habitats with high density would be sufficient to play its role. Lastly, if density-independent mortality is reduced further, the population will be regulated by large density-dependent mortality (Fig. 20C). The level of equilibrium in such cases will vary according to the mode of density-dependent mortality, that is, the type of reproduction curves or the type of intraspecific competition. Fig. 20 C

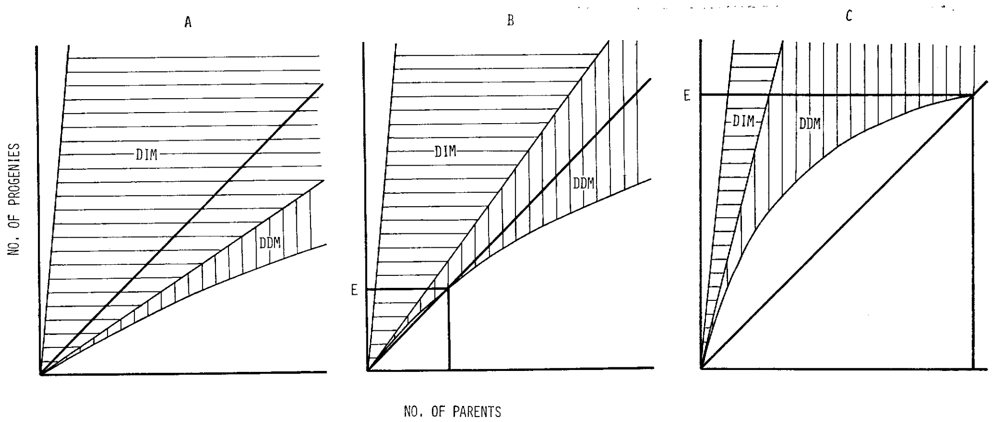

Fig. 20. Schematic representation on the role of density-independent mortality and density-dependent one in population regulation. E : Equilibrium density. DIM : Density-independent mortality. DDM : Density-dependent mortality. For further explanations, see text.

represents only one among various cases. It may be worth mentioning again that A, B and C in Fig. 20 are not types distinct each other but situations being connected through intermediate cases without any interruption. Thus, any animal population can move between two extremes (Case A and Case C) following the environmental change of various time scales such as geological, historical, yearly or seasonal. Various situations may also be observed for local populations belonging to the same species. The population of *Culex tritaeniorhynchus* in our study area is considered to be Case B insofar as the period from 1971 to 1974 is concerned. Therefore, density-dependent processes in a part of rice fields are thought to have been sufficient to regulate the population.

7. Consideration on the Factor Responsible for the Recent Decrease of *Culex tritaeniorhynchus* in Japan

It has been recognized in various regions of our country that *tritaeniorhynchus* populations began to reduce in the end of the 1960's and has been kept at a low level in the 1970's. Nagasaki is not an exception as reported already (Wada *et al.*, 1975). In this circumstance, to make clear the cause of this "accidental" success of control is indispensable to prevent the "accidental" resurgence of the species population.

This decline appears to have following features. Firstly, it occurred throughout Japan. Secondly, the reduction rate is generally very large, although local variation is not small. In Nagasaki, the average level of summer populations is about one fifth of the level before the lowering began, while it is one tenth or frequently much less in other regions. Thirdly, it began in the late 1960's rather suddenly. These features are reflected well in the number of human JE cases; they used to occur every year in every prefecture of southwest Japan, while complete disappearance from some prefectures is not rare in the 1970's. Fourthly, the reduction is frequently less notable in *Anopheles sinensis* than in *tritaeniorhynchus*. This fact was reported from Toyama (Kamimura and Watanabe, 1978), and was observed in Nagasaki, too. Therefore, it is necessary to find factors which can explain these features well.

As discussed in the preceding section, the change in population levels of *tritaeniorhynchus* is attributable to changes in the rice culture system and/or rural environment such as water management of rice fields, chemicals applied to rice fields, livestock and natural enemies. They are responsible for the change in the mean number per unit area of the rice field area. However, another important factor may be involved when we compare population levels between/among different periods or different regions. This is the area of rice fields itself. In the valley including our study area, rural environment including rice fields has been preserved very well, being not influenced seriously by urbanization or disasters. No distinct changes occurred in the general landscape of this area at least for the last 15 years. Therefore, this is a good place to examine the effect of factors other than the reduction of rice fields by urbanization. Here could be recognized two distinct changes about the beginning of the 1970's, that is, the change in the kind of chemicals applied to rice fields and the increase of uncultivated fields. These two will be examined first.

7.1 Changes in Chemicals Applied to Rice Fields

Many kinds of chemicals are applied to rice fields. For instance, more than 40 kinds of active ingredients were consumed in the rice field of Nagasaki in 1972. They include at least 17 kinds of insecticides, 16 of fungicides and 11 of herbicides, and were used not only singly but also as mixtures of two or even more active ingredients. Further, each ingredient or their mixtures may have been sold in different forms (dust, granules, emulsion, wettable powder and so on) containing active components in different rates. Thus, about 40 active ingredients in more than 100 different forms were applied to rice fields of Nagasaki in 1972. This situation makes it quite difficult to know the total amount of each active ingredient applied to rice fields. Therefore, in Fig. 21, only the amount of main chemicals in their most popular market forms are shown to illustrate the transition in the kind of chemicals applied to the rice field of Nagasaki since 1957.

It is very clear that a drastic change in the kind of chemicals occurred in the rather short period from the end of the 1960's and the beginning of the next decade. As for insecticides, carbamate ones or their mixtures with MEP or cartap replaced BHC and its mixtures, following the prohibition of BHC application to rice fields in 1971. Prior to this, application of organic mercury to fields was also prohibited in 1970*, and its place as a fungicide was taken by antibiotics, organophosphori and organochlorines. In the case of herbicides, the strong restriction for the usage of PCP has excluded it from rice fields virtually since 1972, its substitutions being benthiocarb, CNP and NIP. In short, the beginning of the 1970's is just the period in Japan when various laws were made one after another to stop the increasing pollution of environment by chemicals.

The change in the kind of chemicals can influence the population level of *tritaenio-*

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*The production was stopped in 1968.

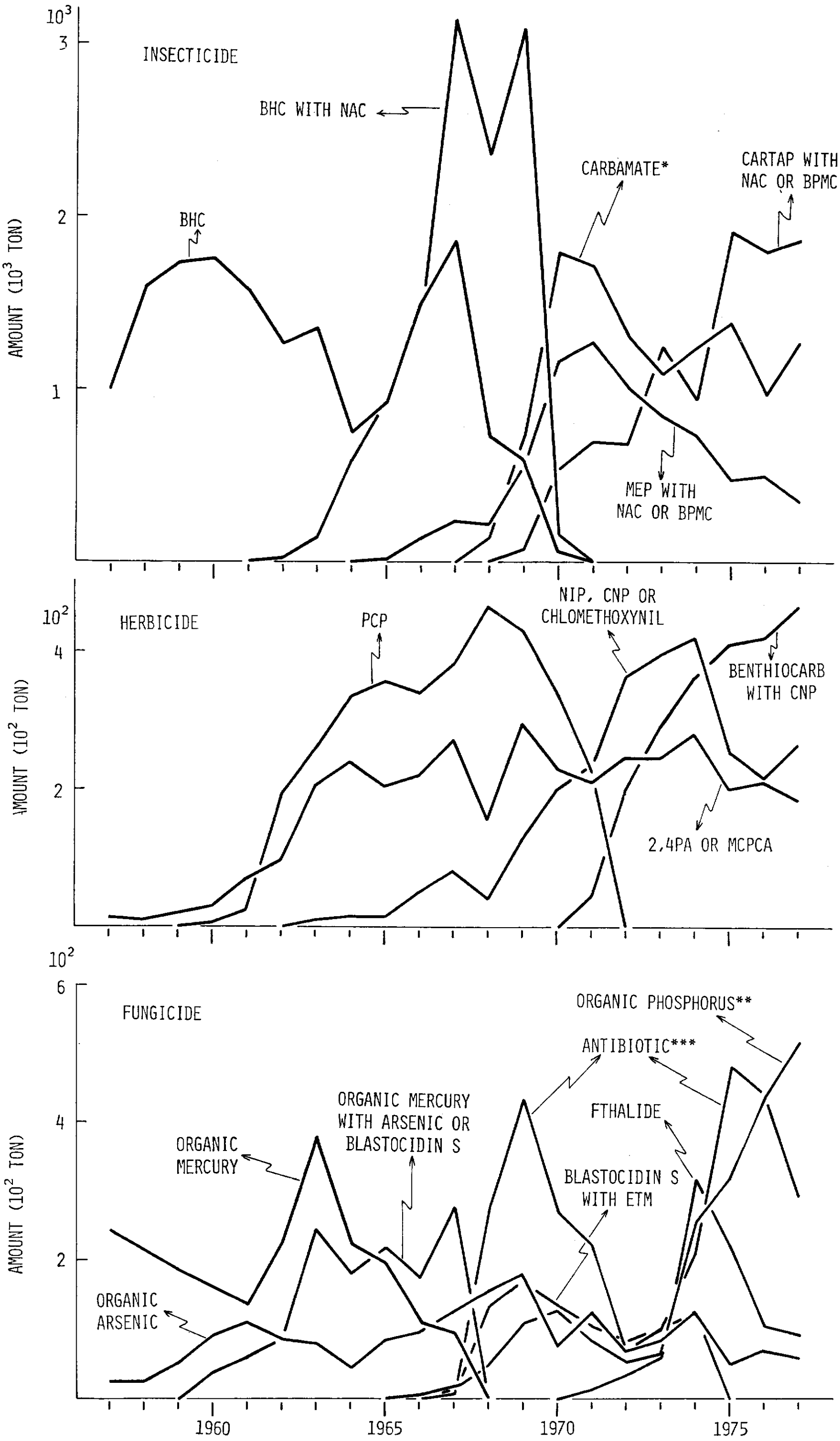

Fig. 21. Amounts of chemicals applied to rice fields of Nagasaki, based on data totalled by Nagasaki Prefectural Office. *: MTMC, BPMC, PHC. **: IBP, EDDP. *** : kasugamycin, blastocidin S, validamycin A.

rhynchus both directly and indirectly, that is, directly through different efficiency in killing mosquitoes and indirectly through difference in effects on other organisms, especially on natural enemies. A series of experiments by Japanese investigators (Yasutomi, 1962; Suzuki and Mizutani, 1962; Maeda and Matsuyama, 1967; Moriya et al., 1969 and Buei and Ito, 1974) revealed that *tritaeniorhynchus* larvae in Japan had developed resistance to BHC and had become generally more susceptible to organophosphorous insecticides (MEP, diazinon and so on) than BHC. The maximum LC-50 value of BHC was 0.67 ppm observed for a strain from Kanagawa (Moriya *et al.*, 1969). In rice fields, a standard application rate per 10 a was 3-4 kg of dust which contains γ-BHC at the rate of 0.03. This application rate gives a theoretical concentration of about 1 ppm if the insecticide drops into water of 10 cm in depth without loss. This calculation suggests that the effect of BHC on resistant *tritaeniorhynchus* may be influenced in the field by various conditions affecting both dropping rates and water depth, for instance the thickness of rice plants and the manner of water management, much more strongly than organophosphorous insecticides. Many larvae may survive the attack of BHC when the dropping rate is low. Therefore, in the region where organophosphorous insecticides became dominant as post-BHC insecticides, increased mortality due to this may be one important factor responsible for recent small populations of *tritaeniorhynchus* (see Buei *et al.*, 1977 and Shimizu, 1974, as to situations in Osaka and Wakayama, respectively). Also in Nagasaki, the increased amount of MEP may be unfavourable to *tritaeniorhynchus*.

Data are scanty about the effectiveness of carbamate insecticides or cartap on *tritaeniorhynchus*. According to Moriya *et al.* (1969), NAC (Sevin in their report) is inferior to BHC in its effect on the species larvae. The LC-50 value was larger than 2 ppm, this concentration being unattainable by the standard application rate of NAC even when the dropping rate is 1.0. On the other hand, Kamimura and Katori (1969) observed that the adult number decreased drastically following the application of NAC (carbaril in their report) at the dosage which gives a theoretical concentration of 0.45 ppm if water depth is 10 cm and the dropping rate is 1.0. Therefore, NAC may be more effective to the adult than the aquatic stages. No published data are available about the effectiveness of other carbamate insecticides on the species, although it was often observed that aquatic stages of the species disappeared completely after the application of some carbamate insecticides (see Section 6.6.14). Also, nothing is known about the effect of fungicides on the species.

Moriya et al., (1969) recognized that the death of *tritaeniorhynchus* larvae due to PCP, a dominant herbicide in the 1960's, occurs at the dosage higher than 10 ppm. This was confirmed also by Shim and Self (1973) who obtained 20.9 as the LC-50 value for the species larvae in Korea. A standard application rate of PCP (3 kg of granules containing the active ingredient at the rate of 0.25) gives a theoretical dosage of 7.5 ppm if water depth is 10 cm. Therefore, the lethal effect of PCP on *tritaeniorhynchus* larvae may be rather small, if any. In fact, Shim and Self (1973) observed that PCP applied at the dosage of this level did not kill the species larvae. Also, they reported that 2,4PA is less lethal than PCP to the species larvae. On the other hand, NIP and CNP, both successors of PCP, were shown to be considerably toxic to *tritaeniorhynchus* larvae (Maeda *et al.*, 1974). LC-50 values of NIP and CNP (MO in their report) for the fourth instar larva were 0.068 and 0.045 ppm, respectively, while the expected concentration in the field is about 2.5 ppm when water is 10 cm in depth (a standard application rate per 10 a is 3-4 kg of granules containing the active ingredient at the rate of 0.07). Therefore, replacement of PCP with NIP and CNP may be more or less responsible for the reduced population of the species in the 1970's.

Effects of chemicals on natural enemies for *tritaeniorhynchus* have scarcely been studied. An only exception may be studies on influence of various insecticides on spider populations, which were done in the field of agricultural entomology, especially by the school of Kiritani (Kiritani, Inoue *et al.*, 1972 ; Kawahara *et al.*, 1971 and so on). Essence of their study interesting in relation to this discussion may be summarized as follows; BHC is incomparably toxic to spiders among tested insecticides including MEP, cartap and carbamate ones, thus replacement of BHC with other insecticides, especially carbamate ones which are relatively safe for spiders, results in recovery of spider populations which were seriously damaged by BHC. In view of possible importance of spiders as predators for *tritaeniorhynchus* (see Section 6.6.14.3), the increased population level of the former is expected to lower the population level of the latter. Effects of chemicals on aquatic predators in rice fields are little studied except for toxicity on fishes. PCP is incomparably toxic to fishes* among chemicals extensively applied to rice fields. Recent recovery of some arthropod predators may also be expected, in view of the developing tendency to prefer chemicals less toxic to non-target organisms.

It may be worth mentioning here that even small increase of predator numbers can result in a considerable change in the population level of *tritaeniorhynchus*, because mortality due to predators is multiplied day by day as far as predators live. Suppose a population where daily mortality is 0.3 and a half of the mortality (0.15) is attributed to predation due to natural enemies, for instance. Increase of the predator number to one and a half times will be followed by increased daily mortality of 0.225 due to predation, thus total daily mortality will be increased to 0.375. In other words, the daily survival rate will be reduced to 0.625 from 0.7. The effect of this change is profound, because the survival rate after 10 days is reduced to 0.009 from 0.028, that is, the number of survivors after 10 days is reduced to only one third of the former level. One and a half times increase of predator populations would be very difficult to be recognized by field observation, in view of yearly fluctuation in predator numbers, biased distribution of predators and also extreme variability of efficiency in collecting aquatic predators by dippers (see Section 6.6.15.2). Therefore, lack of easily appreciable increase of natural enemies is not necessarily a full ground to deny the possibility that the increased number of natural enemies is a very important factor responsible for recent decrease of rice field mosquitoes in our country.

The above consideration may be summarized as follows; replacement of formerly dominant agricultural chemicals with ones being more effective to *tritaeniorhynchus* and less toxic to natural enemies can be a major factor responsible for recent decrease of the species in our country, although the evidence is fragmentary at present. Frequent smaller reduction rates in *Anopheles sinensis* may also be explained well by this. As *sinensis* is generally more tolerable or resistant to chemicals than *tritaeniorhynchus* at least in the larval stage (see Section 6.6.

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*For this reason, PCP was excluded from rice fields.

14), it may be influenced by the change in the kind of chemicals but less severely than *tritaeniorhynchus*.

The above consideration is followed by the further supposition that the appearance of BHC, organic mercury and PCP may have been followed by the reverse event, that is, the raise of population levels of *tritaeniorhynchus*. Their first use in rice fields of Japan was in the following years ;

BHC in 1949,
organic mercury in 1953,
PCP in 1959.

Their prevalence was so rapid that the fundamental control schedule depending on chemicals was seen already in the early 1950's, being completed at the beginning of the 1960's by inclusion of PCP. Although various traditional control measures were available till then, they were not so easy and effective as modern chemicals. Thus, the appearance of synthesized organic insecticides and other chemicals has been well recognized as one of the largest events in development of the rice culture system in our country. However, there seem to be no mosquito surveys which covered around this period of an agricultural revolution. It is very difficult to know the population trend of *tritaeniorhynchus* in the early 1950's directly. On the other hand, the number of human JE cases has been recorded since the middle 1920's without interruption. For a sufficiently short period, the case number may roughly be proportional to the population size of the vector, but changes in other conditions influencing the case number may be very large when a longer period is considered. Besides, there are too many problems on the reliability or meaning of the case number in old times (present criteria for authorizing human JE cases was established in the middle 1960's). Therefore, we must be very careful when we examine the long-term trend in the prevalence of JE. After bearing these points in mind, I will dare to consult statistics of human JE cases. Actual data are seen in various Japanese literature, so they are not reproduced here.

There seems to be recognizable a tendency that the number of human JE cases in our country was kept at a high level constantly during two decades beginning at 1951 as compared with usual years (years other than outbreak ones) before the period as well as after it. As seen above, two decades beginning at 1951 are just the period when BHC, organic mercury and PCP were applied to rice fields in our country very extensively. Therefore, the above tendency, if true, suggests a possibility that the population level of *tritaeniorhynchus* rose following the introduction of modern chemicals, although different explanations may also be possible. The idea that the population level of *tritaeniorhynchus* rose in accordance with the introduction of synthesized organic insecticides may look somewhat strange at first, because we are apt to imagine that mosquitoes were generally more abundant when modern weapons against mosquitoes were yet unavailable. However, the rise of population levels or even the appearance of new pests following insecticide application has frequently been observed in the field of agricultural entomology, and elimination of natural enemies has been regarded as a factor most responsible for the phenomena (Ripper, 1956 and so on). As generally known, one important character common to insects to have got advantage under the attack of chemicals is short generation time with high fecundity, and this is also common to *tritaeniorhynchus*. Besides, great ability to fly of the species (see Section 6.6.17) is considered to be a very important character for the species to survive the attack of chemicals. For further discussion on this problem, see Section 8.1.

Further, some may give the case of malaria as an evidence for the general abundance of rice field mosquitoes in the earlier period, since endemic malaria was nearly eradicated from Japan proper in the early 1950's and its vector *Anopheles sinensis* is a representative of rice field breeders (see Section 4). It is considered, however, that the eradication of malaria from Japan proper is attributed largely to the decreased opportunity for *Anopheles* to bite man due to various changes both in the mode of human life and the environment around human dwellings. Therefore, the prevalence of malaria in the past does not necessarily mean that the density level of *Anopheles sinensis* per unit area of rice fields was much larger than at present.

7.2 Increase of Uncultivated Rice Fields

Generally speaking, increase of uncultivated fields is considered to be unfavourable to the breeding of *tritaeniorhynchus*. Firstly, it reduces the area of breeding places directly. Secondly, the pupation rate is generally lower there than in cultivated fields (see Section 6.3). Thirdly, they probably serve as refuges for spiders (see Section 6.6.15.3). However,

Table 21. Frequency distribution of the larval (pupae inclusive) number per dip in cultivated (and uncultivated) rice fields

No. per dip	*Culex tritaeniorhynchus*				*Anopheles sinensis*			
	1971	1972	1973	1974	1971	1972	1973	1974
0	2,375(75)	2,551(166)	2,083(289)	2,027(162)	1,785(64)	2,018(137)	1,513(231)	1,504(151)
1− 10	273(16)	123(22)	252(66)	47(18)	836(27)	648(51)	765(142)	569(35)
11− 20	26(1)	4	14(6)	1(3)	64(1)	11(6)	51(7)	2(2)
21− 30	9	(1)	8(5)	(1)	7	1	14(1)	
31− 40	5	1(3)	1(2)	(2)	5	1	6(1)	
41− 50	5	(1)	1(2)	(1)	3		5	
51− 60	1		(1)					
61− 70	1		1(1)				2	
71− 80	1		(1)				2	
81− 90	1		(1)					
91−100	1		(1)					
101−150	2		(5)				1	
151−200		(1)						
201−250				(1)				
251−300			(1)					
301−350			(1)					
351−400								
401−450								
451−500							1	

these effects may be rather small in quantity to explain drastic decrease of *tritaeniorhynchus* populations, since the absolute number of the species is generally much smaller in uncultivated fields than in cultivated ones (see Section 6.2). Therefore, this may be a factor common but of minor importance.

In relation to the second point mentioned above, it is interesting that *Anopheles sinensis* did not tend to concentrate in small pools in uncultivated fields in contrast with *tritaeniorhynchus* (Table 21). Higher density was observed in cultivated fields without exception. *Sinensis* lacks a preference for small pools with abundant organic matter. Therefore, relative importance of uncultivated fields as breeding places was much smaller in this species than in *tritaeniorhynchus* (Table 22). Consequently, *sinensis* may be influenced by expansion of the uncultivated area less seriously than the latter. This may be a cause for the small reduction rate in *sinensis*, although a minor one.

Table 22. Numbers* (and %) of immature *Culex tritaeniorhynchus* and *Anopheles sinensis* collected in cultivated fields and uncultivated ones

Year	*Culex tritaeniorhynchus* in			*Anopheles sinensis* in		
	Cultivated field	Uncultivated field	Total	Cultivated field	Uncultivated field	Total
1971	2556 (96.54)	92 (3.46)	2658	4038 (97.68)	96 (2.32)	4134
1972	462 (53.10)	408 (46.90)	870	2270 (90.87)	228 (9.13)	2498
1973	1259 (36.37)	2203 (63.63)	3462	4952 (89.45)	584 (10.55)	5536
1974	155 (25.20)	460 (74.80)	615	1677 (95.07)	87 (4.93)	1764

*Actual numbers collected by dippers.

7.3 Other Factors

The above two are common throughout the rice field area in our country. Besides them, various factors are thinkable. Kamimura and Watanabe (1973) suggested the importance of such changes as the increased number of rice fields where drainage is done, the spread of earlier season transplanting, the prevalence of aerial spraying of insecticides, the concentration of livestock in a small number of large farms with more closed structure than traditional small ones, and the increased number of light traps at animal sheds. Also, Nakamura (1977) suggested the possibility that decrease of both the area of rice fields and the number of animal sheds is responsible for reduction of *tritaeniorhynchus* in Osaka. In short, they attached importance to the decrease of suitable breeding places (due to either the change in water management or the decrease of the area of rice fields) and of available hosts. As seen in earlier sections, there is no doubt that they are very important factors influencing the population level of the species in our country. However, these changes, especially in water management and the area of rice fields, did not necessarily progress remarkably in the beginning of the 1970's throughout Japan. In our study area, for instance, no such changes were recognizable, at least in the scale which can reduce the population level of the species to one fifth or even less of the preceding level. Therefore, they are considered to be factors whose importance in recent decrease of *tritaeniorhynchus* varies locally.

7.4 Conclusions on Factors Responsible for Recent Decrease of *tritaeniorhynchus* in Japan

The foregoing discussion may be summarized as follows.

Factors which are common throughout our country:

Major	(1)	Change in the kind of chemicals applied to rice fields
Minor	(2)	Increase of uncultivated rice fields

Factors whose importance varies locally:

Less local	(3)	Concentration of livestock in a small number of large farms with more closed structure than traditional animal sheds
	(4)	Prevalence of light traps at animal sheds
Very local	(5)	Improvement of water management
	(6)	Prevalence of earlier season transplanting
	(7)	Prevalence of aerial spraying of chemicals for agricultural pests
	(8)	Decrease of rice fields by urbanization

The factors except for the last one are responsible for the change in the density level per unit area of the rice field area. Therefore, it may be concluded further that recent decrease of *tritaeniorhynchus* populations in our country was induced primarily by the decreased density per unit area of the rice field area due to increased mortality following the change in the kind of chemicals applied to rice fields, that is, replacement of formerly dominant chemicals with ones being more effective to *tritaeniorhynchus* and less toxic to natural enemies. This reduction of the density may have been intensified frequently by the decreased availability of host animals and less frequently by some changes in the rice culture system such as improvement of water management. The population may have been reduced further by the decreased area of rice fields in the suburbs of large cities where urbanization progressed rapidly.

If this consideration is correct, the *tritaeniorhynchus* population in our country may keep a present low level under the maintenance of general circumstances at present. However, resurgence of the species population is possible when it has developed strong resistance to carbamate and/or organophosphorous insecticides. Fortunately, the strain strongly resistant to these insecticides has not been reported from Japan proper so far, but the appearance of resistant strains may not be a future problem but a present one in view of striking ability for insects to aquire resistance to insecticides (Brown and Pal, 1971). If recovery of natural enemies is more important than the direct effect of insecticides on *tritaeniorhynchus*, danger of the resurgence would be much smaller.

8. Consideration on the Method to Control *Culex tritaeniorhynchus* in Japan

The most remarkable success in the control of mosquitoes was brought about by residual spraying of insecticides and/or destruction of larval breeding places. Both the plans, however, can not be applied to the control of *tritaeniorhynchus* at least in our country. It was proved by Nishigaki (1970) that residual spraying can not reduce the species population effectively, because of a highly exophilic habit of the species. Also, destruction of larval breeding places is impossible without revolutionary changes in the rice culture system, for instance, replacing paddy field rice plants with upland ones or the breeding of rice plant strains which grow in winter. Of course, the effective breeding area can greatly be reduced by appropriate management of water, but this seems to be rather impractical at present (see Section 8.2). Therefore, it is necessary to find alternative methods. Here are included two problems. One is how to reduce the population when it temporarily has reached or is reaching to a serious level, and the other is how to keep the mean population level low enough to prevent JE virus from prevailing in the pig population. As established well by numerous investigations since Scherer *et al.* (1959), the infection cycle of JE virus is maintained between the domestic pig and *tritaeniorhynchus* at least during the summer epidemic season in our country. Both man and horses, which may suffer from encephalitis, are terminal hosts from which new infection can not be produced. Therefore, prevention of the JE epizootic in pigs may be the most fundamental among methods toward the prevention of human JE cases.

8.1 Methods to Reduce the Population Temporarily

At present, insecticide application to rice fields is the most practical and effective method to reduce *tritaeniorhynchus* populations immediately when necessary. In fact, not a few studies were done to find both effective insecticides and application forms (Asahina *et al.*, 1963; Ogata and Nakayama, 1963a, b; Uemoto, 1969; Nishigaki, 1970 and so on), and a part of the results were applied to practice successfully. However, the theoretical bases were not necessarily very sufficient. Therefore, some theoretical consideration will be given below on the way how to use insecticides to control the species most effectively. For the purpose, a very simple model is introduced. Assumptions set up are as follows:

(1) The whole area is composed of a subareas with equal value for the breeding of *tritaeniorhynchus*.

(2) The mosquito population has distinct generations and increases R times every generation unless controls are practised.

(3) In each generation, controls are practised in b subareas, where no adults emerge.

(4) Controls are done following the regular order of subareas, therefore one subarea is not subjected to controls for successive two generations when $b \leqq a/2$.

(5) The effect of controls is confined within one generation.

(6) The rate of adults staying in the subarea where they have emerged is c, and the emigration rate is d, that is, $d=1-c$.

(7) Adults having left the birth place lay eggs equally in all the subareas, that is, a part of emigrants return to the birth place when they lay eggs.

(8) Only females are considered.

When controls are not done, the total number of adults in the generation t is,

$$TN(t)=\sum_{i=1}^{a} N(t,\ i) \qquad \cdots\cdots (25)$$

Where $N(t,\ i)$ is the number of adults which can be produced in the subarea i at the generation t. If controls are done in b subareas, the number of mosquitoes killed before emergence is,

$$DN(t)=\sum_{i=1}^{b}N(t,\ i) \quad \cdots\cdots (26)$$

thus, the number of adults is reduced to,

$$LN(t)=TN(t)-DN(t)=\sum_{i=b+1}^{a}N(t,\ i). \quad \cdots\cdots (27)$$

Respective numbers of adults staying in and emigrating from the birth place are,

$$SN(t)=c\cdot LN(t)=c\cdot\sum_{i=b+1}^{a}N(t,\ i) \quad \cdots\cdots (28)$$

and

$$MN(t)=d\cdot LN(t)=d\cdot\sum_{i=b+1}^{a}N(t,\ i). \quad \cdots\cdots (29)$$

By Assumption (7), the number of adults immigrating into each subarea when lay eggs is $MN(t)/a$. Therefore, the number of adults which can be produced in the generation $t+1$ is,

$$N(t+1,\ i)=R\cdot MN(t)/a \quad \cdots\cdots (30)$$

in each controlled subarea, and

$$N(t+1,\ i)=R\{MN(t)/a+c\cdot N(t,\ i)\} \quad \cdots\cdots (31)$$

in each uncontrolled subarea. When $t\cdot b$ exceeds a, the calculation is continued by returning to the first subarea. For the calculation, the following values were given for convenience sake:

$t=1,\ 2,\ 3,\ 4,\ 5,$
$a=10,$
$b=0,\ 1,\ 2,\ 3,\ 4,\ 5,\ 6,\ 7,\ 8,\ 9,$
$N(1,\ 1)=N(1,\ 2)=\cdots\cdots=N(1,\ 10)=1$, thus $TN(1)=10,$
$R=10,$
$c=0,\ 0.5,\ 0.9$, thus $d=1.0,\ 0.5,\ 0.1$, respectively.

Table 23 is an example to illustrate the calculation procedures. In parentheses, are given the numbers of mosquitoes killed by controls before emergence. No adults emerge in these cases. It is clearly seen from serial numbers in respective subareas that various types of population trends can be produced even under very simple assumptions. In this example, six types were produced. No adults are produced in each subarea once or twice during five generations and the center for the active breeding moves constantly every generation. In spite of this unstableness in each subarea, the entire population in the whole area grows steadily every generation, as seen from the total number in each generation. In the field, so many factors are involved that the population trend in each local habitat would not be explained simply. However, temporary extinction of larvae by chemicals and subsequent resurgence due to eggs laid by adult immigrants may be one main process responsible for a rather irregular population trend in each local habitat and also great variability in population trends among local habitats. These phenomena are usual in *tritaeniorhynchus* even when the whole population is growing continually.

Before examining the results, it may be worth mentioning the importance of reproduction

Table 23. An example illustrating the calculation prodedure in the model. A case when $R=10$, $c=0.5$ and $b=3$ is shown.

Subarea	No. of mosquitoes produced (and those killed before emergence*) at the generation					Total	No. of controls
	1	2	3	4	5		
1	(1)	3.5	39.75	(324.13)	705.03	748.28(325.14)	2
2	(1)	3.5	39.75	(324.13)	705.03	748.28(325.14)	2
3	(1)	3.5	39.75	324.13	(2325.73)	367.38(2326.73)	2
4	1	(8.5)	22.25	236.63	(1888.23)	259.88(1896.73)	2
5	1	(8.5)	22.25	236.63	(1888.23)	259.88(1896.73)	2
6	1	(8.5)	22.25	236.63	1888.23	2148.11(8.50)	1
7	1	8.5	(64.75)	125.38	1331.98	1466.86(64.75)	1
8	1	8.5	(64.75)	125.38	1331.98	1466.86(64.75)	1
9	1	8.5	(64.75)	125.38	1331.98	1466.86(64.75)	1
10	1	8.5	64.75	(449.13)	705.03	779.28(449.13)	1
Total	7 (3)	44.50 (25.50)	250.75 (194.25)	1410.16 (1097.39)	7999.26 (6102.19)	9711.67(7422.33)	15

*No adults are produced.

rates in relation to control. In a sense, efforts for control is just the battle against large reproduction rates of pests. Therefore, as reproduction rates increase, more controls would be required to attain the same level of control. It was assumed above that the net reproduction rate is 10 per generation. This rate is very high but possible in *tritaeniorhynchus* populations under favourable conditions. In fact, the population of the species increases often a hundred times or much more during a short period from early summer to the midsummer, the period being equivalent to 2 or 3 generations in summer. It is sure that this large reproduction rate is one main factor which makes the control of the species very difficult.

From Table 24, two possibilities of considerable importance can be suggested. The first is that the more the migration rate, the more the difficulty in controlling the species. For instance, when 10 controls are shared among 5 generations ($b=2$) and all the adults emigrate from their birth places ($d=1.0$), 37,448 mosquitoes are produced during 5 generations, while the number is reduced to 10,128 following the reduction of d to 0.1. Influence of migration rates is more remarkable when the number of controls is larger. For instance, when b is 5 and d is 1.0, the population increases every generation, 3,905 females being produced in total. On the other hand, the population decreases and extincts within 5 generations if d is reduced to 0.1. Thus, it can be said that active flight of *tritaeniorhynchus* (see Section 6.6.17) is another important factor which makes the control of the species very difficult.

The second point which can be suggested from Table 24 is that controls concentrated in one generation can suppress the population growth more effectively than controls dispersed over multiple generations if the cumulative number of controls is equal. For instance, when 9 controls are concentrated in the first generation, the total adults produced during 5 generations is 11,111, irrespective of migration rates. If 10 controls are divided among 5 generations

Table 24. Numbers of mosquitoes produced (and those killed before emergence) under various extents of control and dispersal

d	*b*	Generation					Total	Cumulative No. of controls
		1	2	3	4	5		
1.0	1*	9(1)	81 (9)	729(81)	6,561(729)	59,049(6,561)	66,429(7,381)	5
1.0	2*	8(2)	64(16)	512(128)	4,096(1,024)	32,768(8,192)	37,448(9,362)	10
1.0	3*	7(3)	49(21)	343(147)	2,401(1,029)	16,807(7,203)	19,607(8,403)	15
1.0	4*	6(4)	36(24)	216(144)	1,296(864)	7,776(5,184)	9,330(6,220)	20
1.0	5*	5(5)	25(25)	125(125)	625(625)	3,125(3,125)	3,905(3,905)	25
0.5	1*	9(1)	81(10)	719(88)	6,375(797)	56,577(7,174)	63,761(8,070)	5
0.5	2*	8(2)	62(18)	468(152)	3,452(1,228)	24,928(9,592)	28,918(10,992)	10
0.5	3*	7(3)	45(26)	251(194)	1,410(1,097)	7,999(6,102)	9,712(7,422)	15
0.5	4*	6(4)	28(32)	114(166)	482(824)	2,016(2,804)	2,646(3,830)	20
0.5	5*	5(5)	13(38)	31(94)	78(239)	195(586)	322(962)	25
0.1	1*	9(1)	80(10)	704(97)	6,095(944)	51,836(9,109)	58,724(10,161)	5
0.1	2*	8(2)	60(20)	416(188)	2,376(1,779)	7,268(16,490)	10,128(18,479)	10
0.1	3*	7(3)	41(29)	135(274)	298(1,050)	1,025(1,958)	1,506(3,314)	15
0.1	4*	6(4)	19(38)	24(192)	53(377)	75(457)	177(1,068)	20
0.1	5*	5(5)	3(48)	1(34)	1(12)	0(6)	10(105)	25
any	5**	5(5)	50(0)	500(0)	5,000(0)	50,000(0)	55,555(5)	5
any	6**	4(6)	40(0)	400(0)	4,000(0)	40,000(0)	44,444(6)	6
any	7**	3(7)	30(0)	300(0)	3,000(0)	30,000(0)	33,333(7)	7
any	8**	2(8)	20(0)	200(0)	2,000(0)	20,000(0)	22,222(8)	8
any	9**	1(9)	10(0)	100(0)	1,000(0)	10,000(0)	11,111(9)	9
any	0	10(0)	100(0)	1,000(0)	10,000(0)	100,000(0)	111,110(0)	0

d: Emigration rate. *b*: No. of subareas under the control. *: In each generation. **: Only in the first generation. For further explanations, see text,

equally ($b=2$), suppression of this degree is attainable only when the emigration rate is very low ($d=0.1$) ; when d is 0.5, the total number reaches 28,918, and when d is 1.0, the number increases up to 37,448. It is very interesting that total numbers of mosquitoes killed before emergence are 9, 18,479, 10,992 and 9,362 in respective cases. This means that a great number of killed mosquitoes can not necessarily be regarded as a sign of successful control. In some cases, it may be a sign that the control is ineffective or unsuccessful.

In view of great contribution of natural enemies to reducing *tritaeniorhynchus* populations, it is highly probable that enemy-free rice fields quite suitable for the species are produced after disappearance of residual effects of insecticides. To examine the population trend under this circumstance, Assumption (5) was partly modified.

(5′) The net reproduction rate (R) increases r times in subareas exposed to controls in the preceding generation, but this effect is confined to only one generation after each control.

For the calculation, 2, 3 and 4 were given to r. Net reproduction rates of 20, 30 and 40 are extremely high but still probable when natural enemies are eliminated completely (see Section 6.6.15.2). For convenience sake, the emigration rate (d) was assumed to be 1.0 ($c=0$).

The results are presented in Table 25, where two possibilities of great importance can be seen. Firstly, the more the controls, the larger the population, when r is larger for b. For instance, 248,226 mosquitoes are produced with 70,924 killed ones when r is 3 and b is 4.

Table 25. Numbers of mosquitoes produced (and those killed before emergence) when reproduction rates increase after controls.

r	*b*	Generation 1	2	3	4	5	Total	Cumulative No. of controls
2	1*	9(1)	90(9)	900(90)	9,000(900)	90,000(9,000)	99,999(9,999)	5
2	2*	8(2)	80(16)	800(160)	8,000(1,600)	80,000(16,000)	88,888(17,778)	10
2	3*	7(3)	70(21)	700(210)	7,000(2,100)	70,000(21,000)	77,777(23,334)	15
2	4*	6(4)	60(24)	600(240)	6,000(2,400)	60,000(24,000)	66,666(26,668)	20
2	5*	5(5)	50(25)	500(250)	5,000(2,500)	50,000(25,000)	55,555(27,780)	25
3	1*	9(1)	99(9)	1,089(99)	11,979(1,089)	131,769(11,979)	144,945(13,177)	5
3	2*	8(2)	96(16)	1,152(192)	13,824(2,304)	165,888(27,678)	180,968(30,192)	10
3	3*	7(3)	91(21)	1,183(273)	15,379(3,549)	199,927(46,137)	216,587(49,983)	15
3	4*	6(4)	84(24)	1,176(336)	16,464(4,704)	230,496(65,856)	248,226(70,924)	20
3	5*	5(5)	75(25)	1,125(375)	16,875(5,625)	253,125(84,375)	271,205(90,405)	25
3	6*	4(6)	48(40)	576(480)	6,912(5,760)	82,944(69,I20)	90,484(75,406)	30
3	7*	3(7)	27(45)	243(405)	2,187(3,645)	19,683(32,805)	22,143(36,907)	35
4	1*	9(1)	108(9)	1,296(108)	15,552(1,296)	186,624(15,552)	203,589(16,966)	5
4	2*	8(2)	112(16)	1,568(224)	21,952(3,136)	307,328(43,904)	330,968(47,282)	10
4	3*	7(3)	112(21)	1,792(336)	28,672(5,376)	458,752(86,016)	489,335(91,752)	15
4	4*	6(4)	108(24)	1,944(432)	34,992(7,766)	629,856(139,968)	666,906(148,149)	20
4	5*	5(5)	100(25)	2,000(500)	40,000(10,000)	800,000(200,000)	842,105(210,530)	25
4	6*	4(6)	64(24)	1,024(768)	16,384(12,288)	262,144(196,608)	279,620(209,694)	30
4	7*	3(7)	36(57)	432(684)	5,244(8,288)	62,928(99,636)	68,643(108,672)	35
2	5**	5(5)	75	750	7,500	75,000	83,330	5
2	6**	4(6)	64	640	6,400	64,000	71,108	6
2	7**	3(7)	51	510	5,100	51,000	56,661	7
2	8**	2(8)	36	360	3,600	36,000	39,996	8
2	9**	1(9)	19	190	1,900	19,000	21,110	9
3	5**	5(5)	100	1,000	10,000	100,000	111,105	5
3	6**	4(6)	88	880	8,800	88,000	97,772	6
3	7**	3(7)	72	720	7,200	72,000	79,995	7
3	8**	2(8)	54	540	5,400	54,000	59,996	8
3	9**	1(9)	28	280	2,800	28,000	31,109	9
4	5**	5(5)	125	1,250	12,500	125,000	139,980	5
4	6**	4(6)	112	1,120	11,200	112,000	124,436	6
4	7**	3(7)	93	930	9,300	93,000	103,326	7
4	8**	2(8)	68	680	6,800	68,000	75,550	8
4	9**	1(9)	37	370	3,700	37,000	41,108	9

All the adults leave the subarea where they emerged ($c=0$). r: The increasing rate of reproduction in the subarea where the control was done in the preceding generation. For instance, the reproduction rate doubles when $r=2$. For further explanations, see footnotes for Table 23 and the text.

These numbers of produced and killed mosquitoes are about 2 and 5 times as many as corresponding values when *b* is only 1. Cumulative numbers of controls are 20 and 5, respectively. Here, we find again the situation and that the worst one where a vast number of dead mosquitoes by extensive controls can not necessarily be regarded as an evidence of successful control. If we intend to overcome this bad tendency by increasing the number of controls, extremely extensive controls are required every generation. Thus, there produced is a vicious circle that controls themselves produce the necessity for more extensive controls. The second point suggested from Table 25 is that this danger does not occur when controls are concentrated in one generation. Therefore, co-operative control is quite superior to sporadic one when reproduction rates increase after controls.

Although the assumptions are very simple and values given to the model are not necessarily the best, general trends obtained may not be influenced seriously by these defects. The results can be summarized as follows : (1) It is very difficult to control *tritaeniorhynchus* because it has high ability of both reproduction and flight. (2) Controls concentrated in one generation are more effective than controls divided among multiple generations. (3) When the reproduction rate increases after controls, increased control may result in the outbreak of the species. (4) Controls concentrated in one generation do not produce this adverse effect. These results explain well the fact that the species population increases in summer, despite a considerable amount of insecticides applied to rice pests. They also give a theoretical basis for the foregoing speculation that the population level of the species may have risen following the extensive use of modern chemicals (see Section 7.1).

The timing of controls is a very important problem influencing the effectiveness of controls. The yearly peak population in late July or early August may be composed of mixed generations from the third to sixth (see Section 6.2). Thus, theoretically, this peak can be reduced most efficiently by the co-operative control in late spring when larvae of the first generation grow in rice fields (see Table 24). However, this is impractical in view of extensive migration of the adults (see Section 6.6.17). No regions in Japan proper can be regarded as isolated each other insofar as this nomadic mosquito is concerned. Therefore, the concept of the control belt is also impractical for the species. The population in the treated area would be recovered soon by immigrants from untreated or weakly treated areas, and the longer the duration from the treatment to the midsummer peak, the complete the recovery. In relation to this problem the experiments by Nishigaki (1970) is very instructive. He applied MEP at one week interval in all the rice fields in Matsushima, an islet off the Nagasaki mainland, and suppressed the *tritaeniorhynchus* population completely during April and May when larvae of the first two generations grow, but this could not keep the summer population small; the population recovered a high level immediately after the stop of the treatment, probably due to immigration of adult females from the mainland and also the increased survival rate of the aquatic stages by the complete elimination of natural enemies. Therefore, it may be most effective to apply insecticides at the early time of the summer explosion, that is, in early July in many regions. This timing is also good in the sense that it immediately follows the probable time of JE virus introduction into the pig-mosquito infection cycle in Japan proper (see Section 9.1).

No special application against *tritaeniorhynchus* may be necessary, since many insecticides applied to rice pests are considered to be effective to the species (see Sections 6.6.14, 7.1). However, to stop the summer growth of the species effectively with the side effect of agricultural chemicals, it would be necessary to practise controls simultaneously in as many areas as possible, ideally in all the rice field areas in our country. If this is done, only one control in summer may be sufficient to keep the yearly peak population low enough to prevent the JE epizootic in pigs, at least when the average population level is as low as in these several years. However, it must be remembered that extensive simultaneous control with chemicals (or drainage) influences also natural enemies profoundly, although we do not know precisely how serious the influence is. Therefore, it may be wise that the simultaneous control is done only when the increase of human JE cases is unavoidable unless the control is done.

8.2 Methods to Reduce the Mean Population Level

Theoretically, the answer to this problem can easily be obtained. For instance, *tritaeniorhynchus* populations would be kept at a very low level if drainage were done in all the rice fields with a regular interval of one week. Practically, however, we have to meet many secondary but difficult problems. Control of mosquitoes, however successful it may be, does not yield more rice, therefore modification of the rice culture system, especially the introduction of additional procedures, would not easily be accepted by farmers. In fact, there have been developed no practical rice culture systems aiming at the control of *tritaeniorhynchus*, and the species has wholly been subjected to changes in the rice culture system and other environment in rural areas. As mentioned already (see Section 7), the mean population level of the species has been maintained at a very low level for these several years under the present system of rice culture, therefore it is highly desirable that future changes are adopted after full examinations on their effect on the species population. In view of results of this study, at least the change which may reduce predators for *tritaeniorhynchus* should be avoided. Of course, any change unfavourable to the species is most desirable, if practically acceptable.

In addition to the maintenance or development of rice culture systems unfavourable to *tritaeniorhynchus*, light traps at animal sheds are worth examining on their effectiveness in controlling the species. The light trap has several merits as a tool to control mosquitoes, especially *tritaeniorhynchus* in our country. Firstly, animal sheds are the place where the species concentrates most, since the species takes blood largely from livestock, especially from pigs, cows and horses, at least in Japan. In our study area, for instance, most females are considered to take blood at some of five pigsties (see Section 2), which means that we can restrict our targets to these five pigsties. Secondly, light traps kill many mosquitoes immediately after taking blood from pigs in a viremic state (mosquitoes potentially infected with JE virus), thus they contribute directly to reducing human JE cases and also to disturbing the infection cycle of JE maintained between the pig and the vector. Therefore, if light traps are properly used, there may be expected the prevention of the JE epizootic in pigs, just like residual spraying of DDT to human houses led to the remarkable success in the prevention of human malaria which was transmitted by anthropophilic and endophilic *Anopheles*. Thirdly, the acquisition of resistance to light traps may be very difficult, if we can use the light of special wave lengths sufficiently intense to stimulate all the individuals being photopositive. In this case, the appearance of resistant strains is possible only when there are genetical varieties being insensible or negative to the light of traps. Fourthly, to kill *tritaeniorhynchus* attracted to animal sheds is useful to farmers, because the operation can reduce the case number of both equine encephalitis and pig stillbirths, the latter being caused by the infection of pregnant females with JE virus. This is the reason why light traps are operated at a part of animal sheds at present. Fifthly, light traps are considered to destroy the fauna in rice field areas much weakly than other control measures such as chemicals or drainage, since they kill only a part of nocturnal flying insects, among which predators may be small in number, especially when they are operated in animal sheds. Fishes and spiders, both very important natural enemies for the species, are not influenced by light traps. Sixthly, the operation of light traps takes only a little time and labor. Seventhly, light traps cost only a small amount of maintenance expenses. For instance, one type of light traps now prevailing in our country costs only about 300 yen per trap under the present power rate of electricity even when it is operated for 100 nights which cover the main breeding season of the species in our country. A light trap itself amounts to about 10,000 yen, but it can be used at least for several years under usual conditions. Referring to the cost of insecticides for reference, cartap with NAC, a popular insecticide in Nagasaki at present (see Section 7.1), amounts to about 700 yen per 10 a at a standard dosage. Therefore, the application to all the rice fields in the study area (15 ha) needs 105,000 yen, which is nearly equal to the cost necessary for setting 10 light traps (2 per pigsty) and operating all of them for 100 nights. The last but most practical advantage of light traps is that electricity is available at almost all the animal sheds at the present time in Japan. It is not easy at present to find control measures with so many merits, therefore the light trap may be a most promising tool to control *tritaeniorhynchus* in our country both theoretically and practically. However, there still remain many problems which must be studied before the extensive use of light traps is strongly recommended for the control of the species. For instance, we know nothing about such fundamental problems as the collection efficiency of light traps at animal sheds with open structure (see Section 6.6.12) or the range of genetical variability in the phototaxis of mosquitoes.

8.3 Suggestions for Future Studies toward the Control of *tritaeniorhynchus*

It may be reasonable to develop furture studies along two lines. One is to integrate measures available at present into a practical system, and the other is to develop alternative and better measures.

It can not be too stressed that the best control system will be attainable only through the basic ecological study on both *tritaeniorhynchus* and its environment. Any animal species lives as a member of the biological community, and species influence each other through the fairly complicated web of life. Any control directed to one species can not but influence other species, frequently even more profoundly than its direct effect on the target species, and this side effect may be favourable or unfavourable to the target, often in such an extent as to change its population level considerably. Possible relation among chemicals, predators and *tritaeniorhynchus* is an example showing a part of this complexity in the life in rice field areas (see Section 7.1). Further, both the population and the community show, to a certain extent, a tendency to recover the loss of individuals or the component species. For instance, the reproduction rate of the population is changeable through density-related process, and empty niches in the community may soon be occupied by alternative species. This would be true for *tritaeniorhynchus* and the biological community in the rice field area. Therefore, methods to control the species can not be evaluated rightly only through the number of killed individuals, as illustrated in the preceding section. Criteria for the evaluation should be the extents how much the vector population is reduced and in this way how much the probability of JE infection is lowered, both from the levels without the control. Of course, the control must be attained with the least undesirable side effect on human health, rice pests and rice plants. Besides, there may be not a few economic problems which must be solved before a control system is practically accepted. These are beyond the scope of medical entomologists. Therefore, it is highly desirable that the co-operative study is started under the participation from various fields to establish the best plan to manage rice fields with measures available at present.

On the other hand, the search for alternative and better measures must be continued, too. In this respect, very interesting is the study on mosquito control with mucilaginous plant seeds. This idea, which was first presented by Reeves and Garcia (1969), is considered to have three advantages. Firstly, no accumulation of harmful substance is probable, because seeds and their derivatives can be consumed or decomposed by the natural process. Secondly, the effect is selective, probably confined to small animals with a filter feeding habit. Therefore, small Crustacea are only non-target animals which may seriously be influenced by this method. Thirdly, the development of resistance to this method may be very difficult, since filter feeding is a part of behaviour essential to the mosquito life. It is not clear whether or not this idea is developed to the establishment of a practical method, especially the one applicable to such large breeding places as rice fields. However, this is a good example to show that new methods may be created from the idea which looks rather curious at the first stage in its development. In this sense, any idea, however strange it may be, should not be discouraged. Basic studies from various aspects should extensively be promoted to open a new age in the long history of battles between mosquitoes and man. Generally speaking, the method based on behaviour may be promising in the sense that it can be highly specific to the target species (and its close relatives). Both light traps at animal sheds and mucilage from plant seeds are not exceptions to this.

9. Concluding Remarks

In my first plan, the preceding section was to be followed by general discussion of a considerable length. However, this draft is already so long that it shall be closed with a few short comments.

9.1 On the Status of Japanese Encephalitis in Our Country

The number of human JE cases in our country has been kept at a very low level for these several years, and this may be attributable to the lowered population level of the vector mosquito *Culex tritaeniorhynchus* at least partly, as suggested by many investigators. This low level may be maintained for considerable duration of years if the present system of rice culture is unchanged (see Section 7.4). It must be stressed, however, that this does not remove the danger of a sudden and large recurrence of the JE epidemic. This is a logical conclusion from the following facts. Firstly, the number of pigs, the most important amplifier for JE virus in our country, is not decreased at all, and it may be increased further hereafter. Secondly, various evidences support more and more the idea that JE virus disappears from the pig-mosquito infection cycle in Japan proper during winter and is reintroduced every early summer from the outside of the cycle, probably from southern islands or the continent (Hayashi *et al.*, 1978). Thirdly, the size of the vector population fluctuates yearly following the difference of meteorological conditions, especially temperature and precipitation in summer, even though the other conditions are constant (see Section 6.6.19). Large potential for reproduction will easily lead the species population to explosion under favourable conditions. Therefore, very small or even no epidemics of JE for a considerably long period of years does not ensure small epidemics in the following years at all. If the vector population explodes under a suitable combination of meteorological factors, it immediately will be followed by a large recurrence of the JE enzootic in pigs and naturally of human JE cases. The increased rate of unimmunized people during small or no epidemics possibly increases the morbidity rate among infected people, thus the epidemic may be enlarged further. In this respect, the epidemiological status of this disease in our country is quite different from other mosquito-borne diseases such as malaria or filariasis, since the recurrence of epidemics of considerable scales is quite improbable in these when once the causative parasites are eliminated from Japan. Thus, the preventive system against JE epidemics must be maintained and improved as far as *tritaeniorhynchus* and its preferable hosts being sensitive to JE virus occur in our country. From the entomological point of view, it is most desirable to establish a system of a national scale which watches the population trend of the vector and practises appropriate counter measures when the outbreak of the species is predicted. To do this effectively, it is essential to establish practical criteria of mosquito density for judging the necessity of controls. Data obtained during recent small epizootic (and epidemic) years may be helpful for this purpose.

9.2 On the Status of *tritaeniorhynchus* in Our Country

The *tritaeniorhynchus* population in our country represents only a small part of the whole population of the species with a very wide distribution ranging from Indonesia in the east to west Africa in the reverse. Temperate Japan is one of the northernmost regions where the species can colonize successfully, and the breeding is active only in the midsummer in rice fields, especially those shortly after transplanting of rice plants. Further, the Japanese system of rice culture is very intensive. Therefore, conclusions presented in this paper would not be applicable to the species in other regions. In this respect, I am much interested in the life of the species in regions outside Japan, for instance in the tropics, the probable homeland of the species. Comparative studies on the life of the species under various environmental conditions will be quite useful to deepen our understanding of the species population, through which there may be found better ideas to control the species with methods suitable for natural and artificial conditions in respective regions.

9.3 On the Ecological Method

Some say that a considerable part of the theory presented in this paper is based on inference from fragmentary (even accidental) observations or inconclusive experiments. It is believed, however, that the creation of the theory from available facts is indispensable in the field and/or historical sciences such as ecology to accelerate the development of our knowledge. A *sine qua non* for this type of theory is, I think, not that all the underlying facts were proved experimentally but that there are no facts which proved to be inexplicable by the theory. Thus, many small observations by various persons and in various environmental conditions are fairly useful for evaluating the correctness of the theory. In this sense, any observation, however fragmentary it may be, should not be neglected if it is correct.

> There may be sufficient aquatic predators in certain permanent pools to control the breeding of anopheline mosquitoes effectively. Treatment with such larvicides as D.D.T. will destroy these predators as well as mosquitoes present. Unless larvicidal treatment is repeated on a weekly basis, Culicidae will quickly establish themselves in the absence of their enemies; and pools that had been of little importance as mosquito breeding places will become major centres of anopheline development (Laird, 1947).

Apparently, the theory presented in this citation is quite identical with the one presented in this paper. It is instructive that the author of the paragraph reached the same belief as that obtained in this study through the synthesis of many small but precise observations. This, which is probably one of the earliest alarms raised by mosquito students on an undesirable aspect of synthesized organic insecticides which may occur when they are used wrongly, is a good example in the field of medical entomology to show how fruitful natural history is when it is joined with scientific thought. Ecology is scientific natural history (Elton, 1927), which will continue to be truth however splendidly it is developed by the introduction of modern measures.

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* Translation by the present author

Appendix

List of chemicals referred to in this paper

Japanese common name*	English common name or chemical name
Insecticide	
BHC	BHC, HCH, benzene hexachloride
BPMC	*o*-*sec*-butylphenyl methilcarbamate
MPMC	3,4-xylyl methilcarbamate
MTMC	*m*-tolyl methilcarbamate
NAC	carbaryl
PHC	propoxur, arprocarb
cartap	cartap
diazinon	diazinon
MEP	fenitrothion
PAP	phentoate
chlorphenamidine	chlorphenamidine, chlordimeform
Herbicide	
2,4PA	2,4-D
MCPCA	[(4-chloro-*o*-tolyl)oxy])aceto-*o*-chloroanilide
PCP	pentachlorophenol-sodium
NIP	nitrophen, nitrofen
CNP	*p*-nitrophenyl 2,4,6-trichlorophenyl ether
chlomethoxynil	chlomethoxynil
benthiocarb	benthiocarb
Fungicide	
DTAS	poly[methil-bis(thiocyanato)arsine]
MAC	calcium methanearsonate
MAF	iron methanearsonate
ETM	*N*,*N*′-ethylenebis(thiocarbamoyl) sulfide
fthalide	fthalide
EDDP	ediphenphos
IBP	*S*-benzil diisopropyl phosphorothiolate
blastocidin S	blastocidin S
kasugamycin	kasugamycin
validamycin A	validamycin A

*Names used by the Ministry of Agriculture and Forestry of Japan

長崎地方の水田に発生する蚊の生態学的研究，特にコガタアカイエカについて

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我国における日本脳炎ウィルスの主媒介蚊コガタアカイエカの合理的な防除法を確立するためには，その野外での生態，特に個体数の変動機構を明らかにすることが不可欠である．そこで，同種の主な発生水域である水田に発生する蚊の生態学的研究を行なった．長崎地方の一農村で4年間，毎週1回，幼虫と成虫の消長を調査し，18種の蚊を得たが，優占種はシナハマダラカとコガタアカイエカであった．定期調査および種々の実験と観察の結果に基づき，コガタアカイエカの個体数の季節的あるいは年次的変動に影響する諸要因およびそれらの働きについて詳細に検討し，下記の結論を得るに至った．（1）旺盛な増殖がおこるのは通常，7月，すなわち好適発生水域が拡大し，産卵率や蛹化率が急上昇する田植直後の短期間に限られる．（2）増殖に影響を及ぼす主要因は温度，雨量，水田の水管理方式，吸血源の多寡と分布，水田に施用される農薬および捕食性の天敵であると思われる．これらのうち，個体数の年次変動をひきおこす主因は気温と雨量であり，7月の高温少雨は同種の大発生の原因となり得る．一方，個体数の平均レベルの変化は，残りの四要因（いずれも人の活動に直結しているか，あるいは強く影響される要因）が変化することによりひきおこされると考えられる．(3)上記の諸要因の働きは，いずれも密度非依存的であり，個体数を一定のレベルに調節するために不可欠な密度依存的過程は，幼虫期の過密により生ずると考えられる（以上の諸点については第6・6・19節を参照）．これらの結果に基づき，我国で，近年，コガタアカイエカの個体数の平均レベルが著しく低下した原因について考察を加え，同種に対する致死効果が比較的大きく，逆に天敵類に対する毒性が比較的弱い農薬が普及したことが最も普遍的な原因であると推論した（第7・4節参照）更にコガタアカイエカを防除するための合理的な方法についても検討した．簡単なモデルを用いたシミュレーションにより，殺虫剤や水田の落水により同種を有効に防除するためには．できるだけ広い地域で同時に実施することが肝要であることを示した（第8・1節参照）．また畜舎におけるライト・トラップの広範な活用が，同種の数の平均レベルを低く保つための理論的にも実際的にも有望な方法であることをも示唆した（第8・2節参照）．我国における日本脳炎の疫学的位置は，昆虫媒介性の他の重要な疾病，すなわち，マラリアやフィラリア症とは著しくことなっている．後二者においては，一たび，病原寄生虫を根絶することに成功すれば，大流行の再発は殆んどあり得ないのに対して，日本脳炎の場合には，好適な気象条件下でコガタアカイエカが大発生すれば，いかに長期間の小流行あるいは無流行のあとでも，ただちに大流行がひきおこされるであろう．その時には，大流行が無かった時代における人為ないし自然免疫率の低下により，流行が一層大きくなる可能性が大きい．従って，コガタアカイエカの防除を含む同疾病に対する予防体制は，我国にコガタアカイエカ及び同種が好んで吸血する日脳ウィルスに感受性の高い動物（現在は豚）が在存する限り，保持かつ改善されなければならないであろう（第9・1節参照）．

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