LIFE HISTORY OF *NEUROTHEMIS TULLIA* (DRURY) IN A TROPICAL RAINFED RICE FIELD (ANISOPTERA: LIBELLULIDAE)

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The life history was studied from June 1993 through April 1995 in a rainfed rice field of Bandar Baru District in Kedah, Peninsular Malaysia. Larval growth was more uniform during early instars. Increasing variations of growth were obvious during the later instars, especially in the final instar. Plots of head width against wing bud length and body length enabled instars to be determined. Larval development was asynchronous and a maximum of 8 larval instars was found on one sampling occasion. 4 emergences were observed in 1994, in March, May, July and October. In general emergence was relatively synchronized. The E_{50} values were achieved within the first 38%, 9% and 16% of the total duration of emergences 2, 3, and 4 respectively. A relatively short life cycle, continual breeding and oviposition, synchronous emergence and immediate reproduction after a dry period ensure survival of *N. tullia* in the unpredictable rainfed rice ecosystem.

INTRODUCTION

Neurothemis tullia is a medium sized libellulid, commonly found in tropical rice fields (NAKAO et al., 1972; ASAHINA et al., 1976; EK-AMNUAY, 1982; HECKMAN, 1979). Larvae are found during most part of the year and the adults fly all year round as a result of continuous emergence (HECKMAN, 1979). Together with other species, such as *Acisoma* sp., *Diplacodes trivialis* and zygopterans *Agriocnemis* spp. and *Ischnura senegalensis*, they are suspected to be important predators of leaf and plant hoppers, two serious pests of rice in Malaysia.

Rice field (especially rainfed) dragonflies live in a highly disturbed and dynamic ecosystem. The routine agricultural cycle such as ploughing, draining, applying fertilizers and pesticides, and harvesting activities and desiccation of the habitat brought about by the wet and dry climatic cycle, disrupt the community. However,

larval stages of tropical species are short whereas the adult stage is often protracted (CORBET, 1987). The adults either retire to grasses in and around the rice field or nearby forested area during the dry season (WATANABE, 1986).

Synchrony of development has important implications for survivorship and intraspecific (CROWLEY et al., 1987) and interspecific relationships among coexisting odonates (BENKE, 1976). The growth pattern of both larvae and adults as well as their temporal abundance determines the importance of the species in a specific habitat such as rice fields.

Almost all odonate life history studies documented prior to this study illustrated univoltine (LUTZ, 1968; BENKE & BENKE, 1975; PARR, 1970; INGRAM & JENNER, 1976; PICKUP & THOMPSON, 1984; SAWCHYN & GILLOT, 1974a,1974b,1975; KUMAR, 1984; WISSINGER, 1988a) and semivoltine (CORBET, 1957; CORBET & HARVEY, 1989; KORMONDY & GOWER, 1965; BENNETT & MILL, 1993; JOHNSON, 1986) populations in the temperate regions of the world. *Pseudagrion salisburyense* Ris in South Africa was the only multivoltine species studied that had five generations in two summers (CHUTTER, 1961). In this study, the life history of a multivoltine species *N. tullia,* which occurs in a tropical rainfed rice field in the northern part of Peninsular Malaysia is elucidated. This life history data will provide background information on the special adaptations of *N. tullia* to sustain survival over disturbed, temporary habitats of rice fields.

MATERIALS AND METHODS

RICE GROWING PHASES. – In this study, the categorization of rice cultivation phases adopted was a modification of that of MOGI & MIYAGI (1990) and ABU HASSAN (1994). There were seven phases based on the area of surface water covered by the rice plants as well as the physical conditions of the field. A fallow phase was uncultivated, with short but dense hygrophilous weeds. In a rainfed rice field, this phase was usually the longest phase starting immediately after harvest until the next crop. The ground of plough phase was slightly undulated due to the ploughing process and the tyre tracts left by the tractors. Usually the depth of water was less than 10 cm. A seeding phase was a dry or moist field period when partially germinated rice seeds were broadcasted. No larval sampling was carried out during this phase to avoid scattering the seeds or destroying the germinating seedlings. A young field phase had rice plants commencing soon after germination up to 30 cm high, before tillering. During this phase, the water surface was almost entirely exposed to direct sunlight. At a very early stage of young seedling phase, no larval sampling was carried out as the young plants were easily uprooted while dredging the net. A middle field phase (tiller) had rice plants which had completed tillering but had not eared. The water surface was half-shaded by the plants. Rice plants in the subsequent mature field completely shaded the water surface. This phase commenced when the plants eared, had flower panicles, developed grains and lasted until the yellowing of the grains. A field at a preharvest phase was usually drained to hasten the ripening of the grains and to facilitate harvesting. A harvest phase was included in the fallow phase because harvesting took only a few days. Usually the field was abandoned until ploughing for the next crop. Sometimes the field was ploughed immediately after harvest.

LARVAL SAMPLING. – The study was conducted from 8 June 1993 through 10 December 1994 which encompassed two and a half rice growing seasons. A long handle pond net was dragged in a

standard manner (standard net sweep = S.N.S.), a modification of the method used by LAWTON (1970), which consisted of two drags (back and forth) along a metre path.

An area measuring 200 m × 3 m of a plot in an approximately 0.7 ha rice field was sampled throughout the study. The required sample size was calculated based on a preliminary study and ELLIOT's (1973) formula for an aquatic insect population with a negative binomial distribution. Thirty-three samples were collected once weekly between 0900 hrs and noon.

In the laboratory, samples were washed to remove mud and debris. They were then emptied into a white enamel pan and *N. tullia* larvae were sorted. An ocular micrometer was fixed to a dissecting microscope to measure head width (maximum across the eyes), body length (tip of labrum to the distal end of abdominal appendages) and wing bud length (tip of fore wing to end of hindwing) (PRITCHARD, 1964; LUTZ, 1968; INGRAM & JENNER, 1976) of the larvae. All measurements were made on living organisms in order to avoid distortion of body length resulting from constriction of intersegmental membrane upon preservation. Larval instars were designated numerically in a manner similar to LUTZ (1968) and BENKE (1970; 1976); Final = F, penultimate = F-1, antipenultimate = F-2, etc. in relation to number of moults before emergence. Such a designation is advantageous in comparing species which have inconsistent or unknown total number of larval stages. Larvae were identified using keys of KUMAR (1973a; 1973b), ASKEW (1988), CHOWDHURY & AKHTERUZZAMAN (1981), GARDNER (1954a; 1954b) and HAMMOND (1994). To confirm the identification of young instars, eggs of most species were collected from adult females in the field and were reared in filtered or rice field water in the laboratory at room temperature (± 28°C). These larvae were used as reference specimens. Adult dragonflies were identified using keys of FRASER (1936), ASAHINA (1979), EK-AMNUAY (1982) and were confirmed by the International Institute of Entomology, London. The larvae were returned to the field within two to three days.

The weekly mean population densities, histograms and distributions as well as the correlations of the head capsule, body length and wing bud measurements were analyzed and drawn using the software STATGRAPHIC® (Statistical Graphic System, 1988). The measurements of head capsules of *N. tullia* larvae were used to construct size frequency histograms for each sample. CHUTTER (1961) used a class interval of 0.3 mm for *P. salisburyense* whereas PARR (1970) chose 0.2 mm for *Ischnura elegans* (Vander L.) and *Coenagrion puella* (L.) and BENNETT & MILL (1993) used an interval of 0.025 mm to separate twelve instars of *Pyrrhosoma nymphula* (Sulz.). In this study a class interval of 0.1 mm is used to separate ten larval instars. Although 0.2 mm separated early instars quite clearly, a class interval of 0.1 mm showed a clearer growth of head capsule over the sampling periods. Due to low collection of larvae in weekly samplings, two weeks data were pooled as one sampling date.

EMERGENCE. – Emergence studies were conducted in May 1994 through April, 1995. Once emergence was detected, collection of exuviae was made daily in the sampling area throughout the emergence period. Exuviae were usually found 10 to 40 cm above the water surface, hanging to the leaves or clinging to the stems of the rice plants or weeds surrounding the plot. The majority of the adults emerged at night, some did it very early in the morning as some exuviae found in early morning were still wet. Rice plants and vegetation in the sampling area were searched exhaustively around midday to ensure that all exuviae from larvae that emerged for the day were collected. Exuviae were brought back to the laboratory for counting and identification. They were enumerated daily and converted into mean number of emergences per square metre of the rice field. The rice fields in the study area were dry after 10 December 1994 and the exuviae of the last (fourth) emergence were collected on dense overgrowth (grasses) along a 200 m margin of a drainage canal that ran across the field.

RESULTS

LARVAL GROWTH

The relationship between head width and body length of *N. tullia* larvae as well

as data obtained in the laboratory elucidated a maximum of nine larval instars, F to F-8 (Fig. 1a). The prolarval instar was not collected due to its small size and short stadium. Separating *N. tullia* of head width smaller than 0.6 mm was very difficult because at very young stage most libellulid species look very similar (PARR, 1970). Notwithstanding this, smaller larvae of *N. tullia* from laboratory culture were used as reference specimens to minimize misidentification.

The lengths of wing buds were measured in addition to body lengths. Figure 1b shows the scatter plot of head widths and wing bud lengths. Observation on labora-
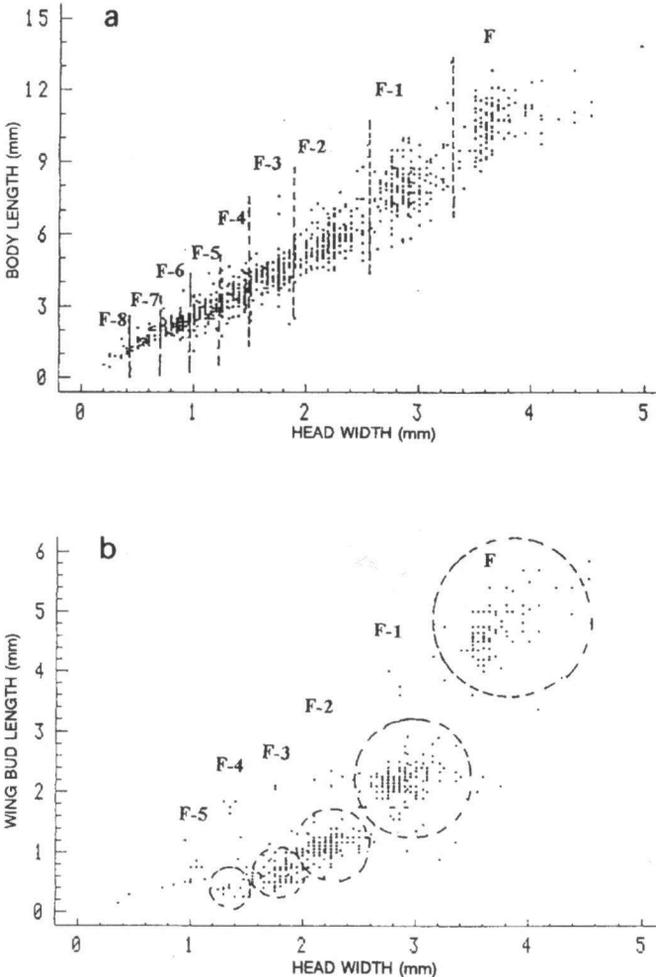

Fig. 1. Relationship between larval head width of *Neurothemis tullia* and (a) larval body length (b) larval wing bud length. – [F to F-8 relates to the number of moults before the larvae reach adult stage. F = final, F-1 = instar nine, F-2 = instar eight, F-3 = instar seven, F-4 = instar six and so on].

tory reared larvae showed that rudiments of wing bud started to grow in instar F-5. Based on the relationship of the head capsule and wing bud lengths in Figure 1b, the last six instars (F-5 to F) were separated even more clearly. According to PARR (1970) large variation in the head width of the final instar was probably due to the size difference of the sexes. However, in this species sexes could not be separated even after thoroughly observing and investigating external body structures of the larvae.

The relationship of body length (BL) and head width (HW) was linear, $BL = 0.3647 + 2.8799HW$ ($R^2 = 94.35\%$, $P = 0.05$, n = 1224) whereas wing bud length (WB) and head width showed a quadratic relationship, $WB = 0.6177 + 0.1804HW + 1.68HW^2$, ($R^2 = 85.44\%$, $P = 0.05$, n = 489).

AGE DISTRIBUTION

Figure 2 shows biweekly size frequency histograms of larval head width for *N. tullia* larvae collected on 22 June, 14 September and 13 October 1993, 4 May, 22 June, 20 July and 3 December 1994. These dates are selected to show large variations in the numerical frequency and the number of instars existing in the field at the various times of sampling. In general, larval development of cohorts was quite synchronized in the earlier stages but towards emergence, as many as eight instars were present simultaneously in the field indicating a continuous breeding and egg hatching. Young larvae entered the population even during emergence.

Completely new populations started three to four weeks after a dry period. An increas-
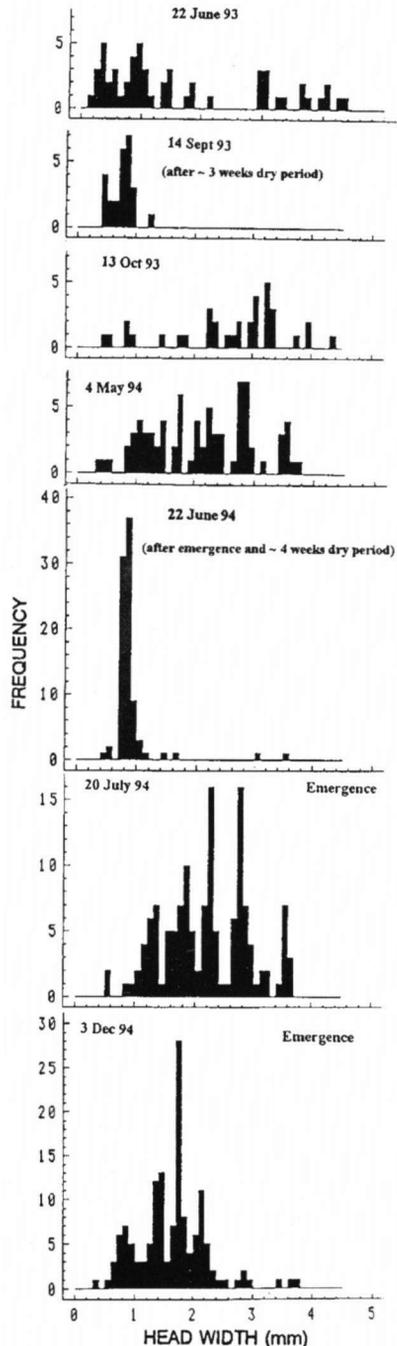

Fig. 2. Age distribution of *Neurothemis tullia* larvae on selected dates in 1993 and 1994.

ing mixture of instar stages was found as the population grew older. Drying of the field was the main obstacle to the continuous growth of the larval population, allowing a maximum of four populations (emergences) to occur in the observed year (Tab. I).

EMERGENCE

Figure 3 shows the patterns of emergence of four generations of *N. tullia* from May 1994 to April 1995. The densities of exuviae were 0.09, 1.14, 0.94 exuviae per m^2 at the first, second and third emergences respectively. The fourth emergence was 0.14 exuviae per metre length of the canal.

Table I lists the dates and durations of all emergences in 1993, 1994 and 1995. Four emergences occurred in 1994 indicating four discrete populations of *N. tullia*. Comparing emergences of the three years, they occurred at approximately the same time of the year although their durations vary.

DISCUSSION

LARVAL GROWTH

The growth of early instars of *N. tullia* was more uniform. An expanding variability in body lengths especially during the last three instars of *N. tullia* indicated
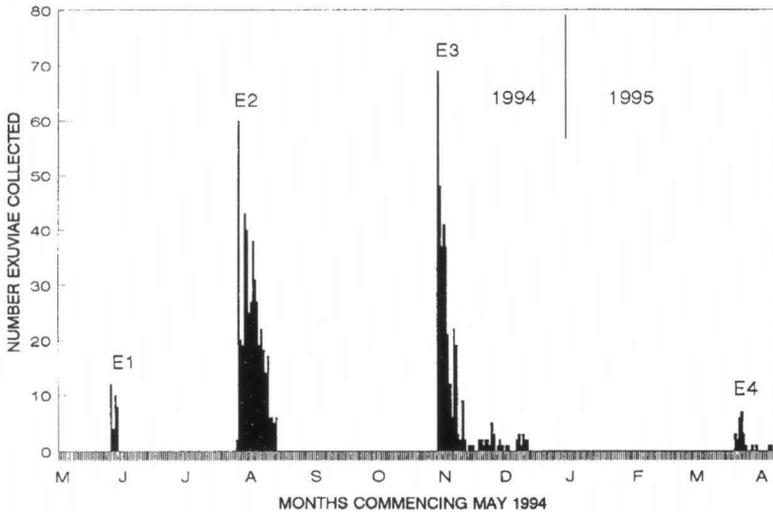

Fig. 3. Patterns of emergence of *Neurothemis tullia* in the rice field. E1 to E4 denotes emergence one to four. E1 occurred in seeding phase, E2 occurred in tiller phase, E3 and E4 occurred in fallow phase of rice cultivation.

Table 1
Emergence periods of different generations of *Neurothemis tullia* in the rice field

1993	1994	1995
-	17 March - 20 April *	18 March - 6 April (E4)
-	25 May - 29 May (E1)	
-	24 July - 12 August (E2)	
20 October - 23 November *	28 October - 10 December (E3)	

*Exuviae were not collected. Emergences were detected by the presence of teneral adults. E denotes emergence. E1 through E4 relate to graphical representation in Figure 3.

that larval development was not uniform among individuals of a similar age group. It is known that differential feeding occurred due to the presence or absence of refugia which determined the prey availability to the individual predator (FOLSOM, 1980; GILLINSKY, 1984). Differential development especially in later instars was also observed in a laboratory reared dragonfly *Anax junius* (BEESLEY, 1972). Different prey preferences between sexes in later instars especially during the final instar could have also caused large variations in body as well as wing bud lengths of *N. tullia* (PARR, 1970).

Young larvae of *N. tullia* were small, their movements limited and their choice of prey was confined to the small arthropods available around them. Therefore their prey species were less varied and consequently their growth was more uniform. It had been observed in many species that the diet of small instar larvae were restricted to limited varieties of small prey around their vicinity (CHUTTER, 1961; CORBET, 1962; THOMPSON, 1978; BLOIS-HEULIN, 1985).

Due to factors such as a greater distance in locomotion, the bigger larvae enjoyed an increasing selection of prey species of different sizes as they grew (CORBET, 1980). Hence bigger larvae of *N. tullia* were exposed to many species of arthropod in the rich fauna of the rice field (HECKMAN, 1979; MOGI & MIYAGI, 1990).

Collections of *N. tullia* larvae in this study were made from five different populations living in different rice phases. The populations of *N. tullia* were higher during tiller, mature and fallow phases as compared to other phases mainly because most aquatic prey were abundant during these times (CHE SALMAH et al., 1995). VAN BUSKIRK (1989) found that crowding resulted in smaller body size of individuals of *Pachydiplax longipennis* (Burm.). Thus it was very likely that *N. tullia* larvae from high density populations also had smaller body sizes. Consequently differences in body size among different cohorts of *N. tullia* contributed towards variations observed in head widths, body lengths and wing bud lengths.

AGE DISTRIBUTION

Neurothemis tullia which occurred in this rice field was a multivoltine, asyn-
chronous breeder with three to seven larval instars present during most sampling
occasions. HECKMAN (1979) postulated that emergence of dragonflies in Thai-
land was continuous and adults were flying throughout the year. There would seem
to be a similar situation for *N. tullia* in the present study. There was only one sam-
pling occasion in one and a half years during which no adult was spotted in the
field.

Asynchronous development was commonly observed in many species of drag-
onflies. For instance CORBET (1957) found that a protracted period of egg laying
of *Anax imperator* Leach caused a wide variation of larval sizes at any one sam-
pling occasion. WISSINGER (1988b) observed that the extended period of ovipo-
sition of asynchronous species *Libellula lydia* Dru., *P. longipennis, Erythemis
simplicicollis* (Say) and *Perithemis tenera* (Say) resulted in late summer larval
populations that contained as many as twelve different instars.

From our observation in the field, *N. tullia* females laid their eggs immediately
after tandem separation. The egg incubation period was eight days in the labora-
tory. This period was assumed to be similar in the field since the eggs of *Coenagrion
puella* (L.) hatched at the same time both in the laboratory and in the field
(WARINGER & HUMPESCH, 1984). The distribution of head widths showed that
young larvae of *N. tullia* can be found in the study field one to two weeks after
emergence. Therefore the maturation period for this species was within the lowest
end of the range for Anisoptera (6 - 40 days). The recruitment period was long, up
to six weeks in March and July, 1994. Consequently an emergence period such as
that of 28 October 1994 was protracted up to six weeks. With a larval development
of seven to twelve weeks (CHE SALMAH, 1996), hatching was obviously con-
tinuous throughout the larval developmental period.

After a dry period (Fig. 3), the very young larvae of *N. tullia* (instars F-9, F-8)
were collected as soon as water was available in the field. The eggs were either laid
immediately after water was available, or there were drought resistant eggs already
in the fields. When the dry period was short (~ four weeks), some muddy pools in
the field served as retreats and a small percentage of the larvae survived the drought
in them. Hence after a short dry period, a few old larvae were still found in the
sample of 22 June 1994.

This study shows that adults bred quickly and larvae grew continuously when-
ever there was suitable habitat. The species is highly adapted in an opportunistic
manner, to the physical and environmental disturbances within the rice field. A
relatively short life cycle allowed the larvae to take advantage of the temporary
habitats available while the adults survived and reproduced all year round.

EMERGENCE

Despite a very asynchronous larval development, emergence of *N. tullia* was relatively synchronous. Fifty percent emergences (E_{50}) were achieved within the first 38%, 9% and 16% of the total emergence durations for emergences two, three and four respectively. It was suspected that some mechanisms operated that led to the synchronization of emergence of *N. tullia*. Larval study in the laboratory showed that the adult of this species could emerge at instar stages 8, 9 and 10 (CHE SALMAH, 1996). Therefore, in order to emerge synchronously, some of the larvae probably omitted a few of the later metamorphic stages. KIME (1974) noted the ability of certain aeshnid larvae to contract their life histories by omitting instars. WISSINGER (1989) also found that larval developments of asynchronous breeders, *Libellula luctuosa* Burm. and *L. pulchella* Dru. were synchronized during the final instars.

According to WISSINGER (1988b), emergence synchrony is generally a good predictor of variability in period of development of larvae. Species with most synchronous larval development (two to three instars at any time), such as *Epitheca cynosura* Say and *Leuchorrinia intacta* Hagen, displayed a short emergence period of about four weeks, whereas that of *Perithemis tenera* (Say), an asynchronous breeder that has a maximum of twelve instar stages lasted for three and a half months.

The synchronization of emergence of *N. tullia* is another adaptive mechanism to overcome the unpredictable environment of the rainfed rice field. Species living in temporary habitats in the tropics usually compromised between smaller body sizes at emergence (in order to emerge faster at the earliest possible instars) and the risk of death due to a 'catastrophe' such as drought (CORBET, 1980). Thus the majority of *N. tullia* larvae quickly emerged to ensure survival to the adult stage.

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REFERENCES

ABU HASSAN, A., 1994. *Studies on the mosquito fauna of Kerian district with emphasis on the man-groveswamp ecotype.* Ph.D. thesis, Univ. Malaya, Kuala Lumpur.

ASAHINA, S., 1979. An illustrated key to the dragonflies found in the paddy field of Thailand. *IABCR-News* 4: 3-10.

ASAHINA, S., T. WONGSIRI & A.NAGATOMI, 1972. The paddy field Odonata taken at Bangkhen, Bangkok. *Mushi* 46: 107-109.

ASKEW, R.R., 1988. *The dragonflies of Europe.* Harley, Martins.

BEESLEY, C., 1972. *Investigation of the life history and predatory capacity of Anax junius Drury (Odonata: Aeshnidae)*. Ph.D. thesis, Univ. California, Riverside.

BENKE, A.C., 1970. A method for comparing individual growth rates of aquatic insects with special reference to the Odonata. *Ecology* 51: 328-331.

BENKE, A.C., 1976. Dragonfly production and prey turnover. *Ecology* 57: 916-925.

BENKE, A.C. & S.S. BENKE, 1975. Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology* 56: 302-317.

BENNETT, S. & P.J. MILL, 1993. Larval development and emergence in Pyrrhosoma nymphula (Sulzer) (Zygoptera: Coenagrionidae). *Odonatologica* 22(2): 133-145.

BLOIS-HEULIN, C., 1985. The larval diet of three Anisoptera (Odonata) species. *Freshwat. Biol.* 15: 505-514.

CHE SALMAH, M.R, 1996. *Some aspects of biology and ecology of Neurothemis tullia (Drury) (Odonata: Libellulidae) in the laboratory and rainfed rice field*. Ph.D. thesis, Univ. Pertanian Malaysia, Serdang.

CHE SALMAH, M.R., A. ABU HASSAN & M.Z.A. RASHID, 1995. *Diversity of aquatic insect in the rice ecosystem, with emphasis on the Odonata in West Malaysia*. Int. Symp. Workshop Conserv. Biol., Univ. Malaysia Sarawak, Kuching, 10 pp. – [Sep.].

CHOWDHURY, S.H. & M.D. AKHTERUZZAMAN, 1981. Dragonfly (Odonata: Anisoptera) larvae from Chittagong. *Bangladesh J. Zool.* 9(2): 131-144.

CHUTTER, F. M., 1961. Certain aspects of the morphology and ecology of the nymphs of several species of Pseudagrion Selys (Odonata). *Arch. Hydrobiol.* 57(4): 430-463.

CORBET, P.S., 1957. The life history of the Emperor Dragonfly Anax imperator Leach (Odonata: Aeshnidae). *J. Anim. Ecol.* 26: 1-69.

CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.

CORBET, P.S., 1980. Biology of Odonata. *Annu. Rev. Ent.* 25: 187-217.

CORBET, P.S., 1987. Dragonflies and their New Zealand representatives. *In*: R.J. Rowe, The dragonflies of New Zealand. Auckland Univ. Press.

CORBET, P.S. & I.F. HARVEY, 1989. Seasonal regulation in Pyrrhosoma nymphula (Sulzer) (Zygoptera: Coenagrionidae). 1. Seasonal development in nature. *Odonatologica* 18(2): 133--145.

CROWLEY, P.H., P.M. DILLON, D.M. JOHNSON & C.N. WATSON, 1987. Intraspecific interference among larvae in a semivoltine dragonfly population. *Oecologia* 71: 447-456.

EK-AMNUAY, P., 1982. *Taxonomy of the family Libellulidae in the central area of Thailand*. M.Sc. thesis, Univ. Kasetsart, Bangkok.

ELLIOT, J..M., 1973. *Some methods for the statistical analysis of samples of benthic invertebrates*. Freshwat. Biol. Assoc. Sc. Publ. No. 25.

FOLSOM, T.C., 1980. *Predation ecology and food limitation of the larval dragonfly Anax junius (Aeshnidae)*. Ph.D. thesis, Univ. Toronto, Can.

FRASER, F.C., 1936. *The fauna of British India including Ceylon and Burma: Odonata*, Vol. 3. Taylor & Francis, London.

GARDNER, A.R., 1954a. A key to the larvae of the British Odonata. 1. Zygoptera. *Ent. mon. Mag.* 5: 157-171.

GARDNER, A.R., 1954b. A key to the larvae of the British Odonata. 2. Anisoptera. *Ent. mon. Mag.* 5: 193-213.

GILLINSKY, E., 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65(2): 455-468.

HAMMOND, C.O., 1994. *The dragonflies of Great Britain and Ireland*. Harley, Martins.

HECKMAN, C.W., 1979. *Rice field ecology in northeastern Thailand*. Junk, the Hague.

INGRAM, B.R. & C.E. JENNER, 1976. Life histories of Enallagma hageni (Walsh) and E. aspersum (Hagen) (Zygoptera: Coenagrionidae). *Odonatologica* 5(4): 331-345.

JOHNSON, D.M., 1986. The life history of Tetragoneura cynosura (Say) in Bays Mountain Lake,

Tennessee, United States (Anisoptera: Corduliidae). *Odonatologica* 15(1): 81-90.

KIME, J., 1974. *Ecological relationships among three species of aeshnid dragonfly larvae.* Ph.D. thesis, Univ. Washington, Seattle.

KORMONDY, E.J. & J.L. GOWER, 1965. Life history variations in an association of Odonata. *Ecology* 46(6): 882-886.

KUMAR, A., 1973a. Description of the last instar larvae of Odonata from the Dehra Dun Valley (India) with notes on biology. I. Suborder Zygoptera. *Orient. Insects* 7(1): 83-118.

KUMAR, A., 1973b. Description of the last instar larvae of Odonata from the Dehra Dun Valley (India) with notes on biology. II. Suborder Anisoptera. *Orient. Insects* 7(2): 291-331.

KUMAR, A., 1984. On the life history of Pantala flavescens (Fabricius) (Odonata: Libellulidae). *Ann. Ent.* 2(1): 43-50.

LAWTON, J.H., 1970. A population study on larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). *Hydrobiologia* 36: 33-52.

LUTZ, P.E., 1968. Life history studies on Lestes eurinus Say (Odonata). *Ecology* 49(5): 576-579.

MOGI, M. & L. MIYAGI, 1990. Colonization of rice fields by mosquitoes (Diptera: Culicidae) and larvivarous predators in asynchronous rice cultivation areas in the Philippines. *J. med. Ent.* 27(4): 530-536.

NAKAO, S., K. S. ASAHINA, T. MIURA, T. WONGSIRI, G.A. PANGGA, L.H.Y. LEE & K. YANO, 1976. The paddy field Odonata collected in Thailand, the Philippines and Hong Kong. *J. Kurume Univ.* 25(2): 1612-1615.

PARR, M.J., 1970. The life histories of Ischnura elegans (Van der Linden) and Coenagrion puella (L) (Odonata) in South Lancashire. *Proc. R. ent. Soc. Lond.* (A) 45(10-12): 172-181.

PICKUP, J. & D.J. THOMPSON, 1984. The effects of prey density and temperature on developments of larvae of the damselfly Lestes sponsa (Hans.) (Zygoptera: Lestidae). *Adv. Odonatol.* 2: 169-178.

PRITCHARD, G., 1964. The prey of dragonfly larvae (Odonata: Anisoptera) in Northen Alberta. *Can. J. Zool.* 42: 785-800.

SAWCHYN, W.W. & C. GILLOT, 1974a. The life histories of Lestes congener (Odonata: Zygoptera) on the Canadian Prairies. *Can. Ent.* 106: 367-376.

SAWCHYN, W.W. & C. GILLOT, 1974b. The life histories of three species of Lestes (Odonata: Zygoptera) in Saskatchewan. *Can. Ent.* 106: 1283-1293.

SAWCHYN, W.W. & C. GILLOT, 1975. The biology of two related species of coenagrionid dragonflies (Odonata: Zygoptera) in Western Canada. *Can. Ent.* 107: 119-128.

STATGRAPHICS STATISTICAL GRAPHIC SYSTEM, 1988. Statistical graphic system Inc. (User's guide part 1 & 2).

THOMPSON, D.J., 1978. The natural prey of larvae of damselfly Ischnura elegans (Odonata: Zygoptera). *Freshwat. Biol.* 8: 377-384.

VAN BUSKIRK, J., 1989. Density-dependent cannibalism in larval dragonflies. *Ecology* 70(5): 1442--1449.

WARINGER, J.A. & U.H. HUMPESCH, 1984. Embryonic development, larval growth and life cycle of Coenagrion puella (Odonata: Zygoptera) from an Austrian Pond. *Freshwat. Biol.* 14: 385--399.

WATANABE, M., 1986. A preliminary study of the population dynamics of Orthetrum j. japonicum (Uhler) in paddy fields (Anisoptera: Libellulidae). *Odonatologica* 15(2): 219-222.

WISSINGER, S.A., 1988a. Spatial distribution, life history and estimates of survivorship in a fourteen-species assemblage of larval dragonflies (Odonata: Anisoptera). *Freshwat. Biol.* 20: 329--340.

WISSINGER, S.A., 1988b. Life history and size structure of larval dragonfly populations. *Jl N. Am. benthol. Soc.* 7(1): 13-28.

WISSINGER, S.A., 1989. Comparative population ecology of the dragonflies Libellula lydia and Libellula luctuosa (Odonata: Libelllulidae). *Can. J. Zool.* 67: 931-936.