

## Ecology of the *Aedes australis* (Erichson) 1842 Complex (Diptera: Culicidae) in Australia and New Zealand

REINHART A. BRUST

Department of Entomology, University of Manitoba, Winnipeg, Manitoba, R3T 2N2, Canada.  
Present address: #110 13860 70th Ave, Surrey, BC V3W 0S1, Canada.

**ABSTRACT** Most populations of *Ae. australis* developed their first egg batch without a blood-meal (autogeny), but the proportion of females that were autogenous was altered by environmental conditions. Low rearing temperatures were more favourable than high temperatures for autogenous egg development, when combined with a rich protein larval diet. Neither an adult carbohydrate meal nor mating were necessary for maximum autogenous egg production. Of five Tasmania collections examined, the proportion of autogenous females amongst the different populations ranged from 100% to 0%. In the autogenous Sydney, NSW, population, the addition of a blood-meal did not increase egg production in the first gonotrophic cycle.

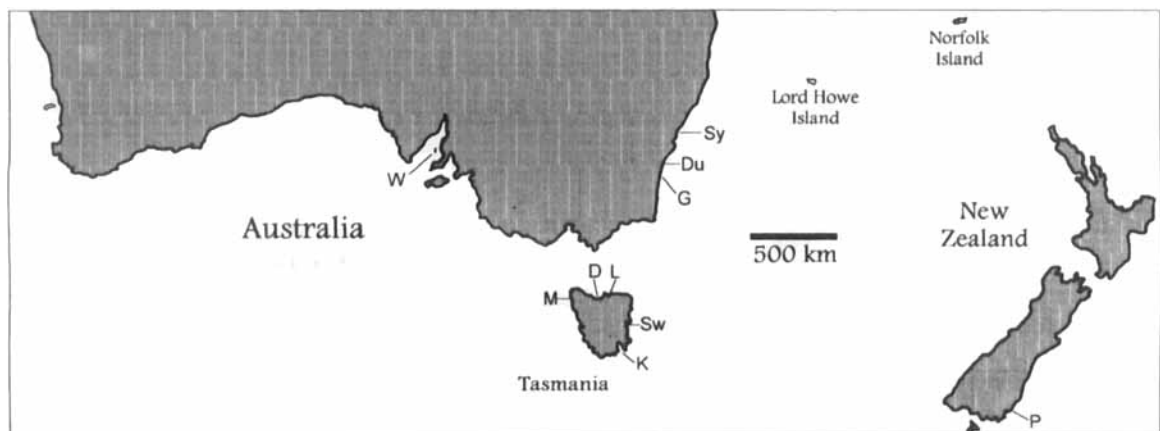
### Introduction

The saline rock pool mosquito *Aedes australis* (Erichson) is a species complex which currently consists of two species, *Ae. australis* and *Aedes ashworthi* (Edwards) (Brust and Mahon 1997). *Ae. ashworthi* occurs in Western Australia, it is anautogenous, and may have diverged from its sibling species *Ae. australis* in eastern Australia in a previous era (Brust and Mahon 1997). *Ae. australis* is distributed along the seacoast from the Queensland/New South Wales border south to Victoria, including Tasmania and islands in the Bass Strait, and west to South Australia. It is also present in Lord Howe and Norfolk Islands, and in New Zealand (Belkin 1968; Dobrotworsky 1966; Lee *et al.* 1984). From the number of collection sites reported in the literature, and from the intensity of the populations at these sites, it appears that Tasmania is the geographical centre of *Ae. australis* in Australasia. Biological, reciprocal crosses of a population from each of South Australia, New South Wales and New Zealand showed that post-mating reproductive

isolation was rare or absent amongst these populations, and that they should be regarded as conspecific (Brust unpubl. data).

Most populations of *Ae. australis* are autogenous, but females are known to feed on humans in nature and have been reported as a pest in eastern Tasmania (Russell 1993). Females from Tasmania and New Zealand have been infected experimentally with Ross River virus, and the NZ population was able to transmit the virus (Austin and Maguire 1982; Kay and Aaskov 1989). The blood feeding habit, versus autogeny (production of eggs without blood) of *Ae. australis* should be investigated from different parts of its distribution to assess its potential as an arbovirus vector.

To understand one aspect of the reproductive biology of the *Ae. australis* complex (*viz.* autogeny versus anautogeny), nine populations from across Australia and one from New Zealand were examined for the ability of females to produce eggs when reared under laboratory conditions favourable to autogenous egg development. Experiments were also conducted to investigate



**Fig. 1.** Map of the sites from which larval populations of the *Aedes australis* complex were obtained. W-Wardang Island, SA; D-Devonport, L-Low Head, K-Kingston, M-Marawah, Sw-Swansea, Tas; DU-Durras, G-Guerilla Bay, Sy-Sydney, NSW; P-Purakanui Bay, NZ.

separately the effects of environmental conditions, an adult carbohydrate diet, mating, and blood-feeding on egg development in autogenous females.

### Materials and methods

Larval collections of *Ae. australis* were obtained from Purakanui Bay (NZ), Sydney, Durras and Guerilla Bay (NSW), Kingston, Swansea, Low Head, Devonport and Marrawah (Tas) and Wardang Island (SA) (Fig. 1). Larvae were transported by air or by road, and were reared under controlled environmental conditions in the laboratory. They were fed liver powder (ICN Biomedicals, Ohio, USA) daily, in excess of consumption, and were reared uncrowded in pans 33 × 33 × 10 cm high. Pupae were removed and placed in clear acrylic cube cages either 32 cm or 15 cm per side. The autogenous populations were stenogamous, and mated readily in either sized cage. Populations that were partially autogenous or anautogenous mated readily when reared and maintained at 16–18 °C, and when more males than females were available. Adults were offered 10% sucrose, and anautogenous populations were fed on a human host. Wing length measurements provide a reliable estimate of body weight (mass) in mosquitoes (Siegel *et al.* 1994), and wing length of adult females was measured from the axillary incision (Harbach and Knight 1980) to the apex of the wing, excluding the wing fringe scales. Statistix® software (Tallahassee, Florida, USA) was used for statistical analyses. Regression analysis was used to compare wing length against egg numbers, wing length against latitude, and latitude against proportion of autogenous females. Minimum and maximum 95% confidence

intervals were used to determine whether means of wing length or egg numbers differed amongst females from different populations.

### Results

When a population at Durras, NSW, developed under natural conditions in the field, there was a difference in the proportion of autogenous females that emerged at the peak of summer as compared to the proportion of autogenous females that emerged from the same pool at the peak of winter, when the temperatures were lower and development was slower. Females that emerged in winter were larger; 85% of the females were autogenous in July, when the rock pool temperatures were low (10–18 °C), while only 40% of the females were autogenous in January, when the rock pool temperatures were much higher (20–32 °C). The number of eggs developed per female was not statistically different between January and July (Table 1).

When the Durras population was reared under controlled environmental conditions of 26 °C and 16L:8D, the adults were smaller, not all females were autogenous, and those that were autogenous laid fewer eggs than populations reared at 16 °C, at either 16L:8D or 10L:14D (Table 2). The different photoperiods had no statistically significant effect on female size nor on the mean number of eggs per female.

The number of autogenous eggs per female was correlated with female size ( $R^2 = 0.39$ ,  $n = 29$ ,  $P < 0.002$ ) (Fig. 2) in females of a Guerilla Bay, NSW population reared in the laboratory at 24 °C. These laid from 58 to 167 eggs (mean 115.4) and wing length ranged from 3.6 to 4.2 mm (mean 4 mm).

**Table 1.** Autogeny in a natural population of *Ae. australis* from Durras, NSW. Pupae were collected in the field and the adults were maintained on 10% sucrose at 16 °C, 10L:14D.

Date of collection	Mean WL <sup>1</sup>	% autogenous	Mean no. of eggs
18 January 1995	3.2 (0.03) a <sup>2</sup>	40	35 (4.1) a
15 July 1995	3.8 (0.02) b	85	41 (3.6) a

<sup>1</sup>Wing length in mm; SEM in parentheses; N = 30/treatment.

<sup>2</sup>Different letters within a column indicate that the means are statistically different (95% C.I.).

**Table 2.** Autogeny in a population of *Ae. australis* from Durras, NSW, under different controlled conditions in the laboratory.

Conditions	Mean WL <sup>1</sup>	% autogenous	Mean no. of eggs
26 °C, 16L:8D	3.8 (0.02) a <sup>2</sup>	85	91 (4.0) a
16 °C, 16L:8D	4.4 (0.02) b	100	137 (5.0) b
16 °C, 10L:14D	4.5 (0.02) b	100	126 (4.0) b

<sup>1</sup>Wing length in mm; SEM in parentheses; N = 30/treatment.

<sup>2</sup>Different letters within a column indicate that the means are statistically different (95% C.I.).

**Table 3.** The effects of mating and of an adult sucrose (10%) meal on autogeny in the Sydney population of *Ae. australis*<sup>1</sup>.

Diet	Mated	Mean WL <sup>2</sup>	% autogenous	Mean no. of eggs
Sucrose	Yes	4.6 (0.02) a <sup>3</sup>	100	119 (2.3) a
Sucrose	No	4.6 (0.02) a	100	121 (3.8) a
Water	Yes	4.5 (0.02) a	100	119 (4.5) a
Water	No	4.5 (0.02) a	100	122 (2.5) a

<sup>1</sup>Rearing and maintenance 16 °C, 10L:14D.

<sup>2</sup>Wing length in mm; SEM in parentheses; N = 30/treatment.

<sup>3</sup>The same letter within a column indicates that the means are not statistically different (95% C.I.).

There was no effect on the expression of autogeny, nor on the number of eggs developed due to the presence or absence of a sucrose meal in females of a Sydney population. Similarly, mating had no effect on the expression of autogeny, nor on the number of eggs developed (Table 3).

When populations from different locations in Australia and one from New Zealand were reared and maintained at environmental conditions favourable to the expression of autogenous egg development, under the same larval and adult food regimes, there was considerable variation in the proportion of autogenous females in the populations. The Wardang Island, Devonport and Low Head females were anautogenous, whereas the Marrawah females were 100% autogenous. The Swansea collection consisted of 13% autogenous females and the collection from Kingston consisted of 5% autogenous females. The most southerly population studied was the one from Purakanui Bay, NZ; it consisted of 4% autogenous females. There was a gradation in the sizes of females by population, with the most southern population being the largest (Table 4). The regression of latitude against wing length  $Y = -2.27 + 8.35X$  was highly significant ( $R^2 = 0.63$ ,  $n = 8$ ,  $P < 0.01$ ). There was a trend towards fewer autogenous females in the more southern populations, but the proportion of autogeny was not well defined by latitude. The regression of latitude against proportion of autogenous females was not significant ( $R^2 = 0.26$ ,  $n = 8$ ,  $P > 0.15$ ).

When females of the Sydney population were offered a blood meal at 3-4 d of age, 14 out of 30 took a full meal when the adults were placed within 1 cm of a potential human blood-meal. By days 8-9, non-blood-fed females developed the same number of eggs as blood-fed females (Table

5). The follicles were all developed to the egg stage, and there were no partially developed follicles in any of the blood-fed females.

### Discussion

Autogenous egg development in mosquitoes is influenced by genetics (O'Meara and Craig 1969; O'Meara 1972; Eberle and Reisen 1986), environmental conditions for rearing and maintenance of the population (Spadoni *et al.* 1974; Brust 1991; Sota and Mogi 1995), nutrition of the larvae (O'Meara and Krasnick 1970), carbohydrate diet of females (O'Meara and Petersen 1985) and presence or absence of mating (O'Meara and Evans 1976). Since genetically autogenous females use stored lipoproteins for egg production, a high protein larval diet is favourable for maximum egg development in the adult female (O'Meara and Krasnick 1970). Environmental conditions influence the expression of autogeny in both *Culex* and *Aedes* species that possess the genes for autogeny. In the temperate climate mosquito *Culex tarsalis* Coquillett, which overwinters as an adult and has an ovarian diapause, high temperatures and long photoperiods during the pupal stage favour maximum expression of autogenous egg development. Low temperatures and short photoperiods induce reproductive diapause and preclude any ovarian follicle development (Reisen 1986; Brust 1991). *Aedes* spp. overwinter primarily as diapausing eggs, and, in contrast to most temperate climate *Culex* spp., adults do not diapause. In *Aedes togoi* (Theobald), low temperatures and short photoperiods are most favourable for autogenous egg production (Sota 1994; Sota and Mogi 1995). In any given year, the last generation adults, prior to the winter season,

**Table 4.** The presence or absence of autogeny, and the collection location and degrees south latitude (°SL) of various populations of *Ae. australis* reared under identical conditions in the laboratory<sup>1</sup>.

Collection location	°SL	Mean WL <sup>2</sup>	% autogenous	Mean no. of eggs
Sydney, NSW	33.8	4.6 (0.02) a <sup>3</sup>	100	119 (2) a
Wardang Is, SA	34.5	5.0 (0.03) c	0	0
Durras, NSW	35.6	4.5 (0.02) a	100	126 (4) a
Marrawah, Tas	40.9	5.2 (0.02) d	100	113 (3) a
Low Head, Tas	41	4.8 (0.02) b	0	0
Devonport, Tas	41.2	4.8 (0.03) b	0	0
Swansea, Tas	42	5.4 (0.03) e	13	80 <sup>4</sup>
Kingston, Tas	43	5.4 (0.03) e	5	77 <sup>4</sup>
Purakanui Bay, NZ	46.5	5.7 (0.02) f	4	85 <sup>4</sup>

<sup>1</sup>Rearing and maintenance 16°C, 10L:14D; adults were fed 10% sucrose.

<sup>2</sup>Wing length in mm; SEM in parentheses.

<sup>3</sup>Different letters within a column indicate that the means are statistically different (95% C.I.).

<sup>4</sup>Insufficient N for statistical treatment.

**Table 5.** Effect of a blood meal on egg production in an autogenous population of *Ae. australis* from Sydney, NSW<sup>1</sup>.

Blood meal	N	Mean WL <sup>2</sup>	% autogenous	Mean no. of eggs
Yes	14	4.6 (0.03) a <sup>3</sup>	100	155 (7.2) a
No	16	4.6 (0.03) a	100	157 (4.9) a

<sup>1</sup>Rearing and maintenance conditions 16°C, 10L:14D; Blood-fed at 3-4 d and dissected at 8-9 d of age.

<sup>2</sup>Wing length in mm; SEM in parentheses.

<sup>3</sup>The same letter within a column indicates that the means are not statistically different (95% C.I.).

have the advantage that they do not need to seek a blood-meal (Sota and Mogi 1995).

Genetically autogenous populations of *Ae. australis* also respond differently to environmental conditions. A population at Durras, NSW had a higher percentage of autogenous females emerging from the same rock pool in winter than in summer (Table 1). The lower winter temperatures were favourable to the production of larger females, from presumably larger larvae with greater lipoprotein reserves. Blood-fed, anautogenous females from Durras laid three times as many eggs as autogenous females when both types emerged from the same rock pool during January (Brust unpubl. data). *Ae. australis* is known to feed on humans, and this blood source would likely be more available in the summer months when humans inhabit the beaches. The peak of anautogenous females coincides with the peak of human activity and it is advantageous for a larger proportion of the population to seek a blood meal in summer.

When the Durras population was reared under controlled environmental conditions, the proportion of autogenous females and the number of eggs developed was lower at 26°C than at 16°C (Table 2). This result paralleled the winter/summer condition in nature, with the exception that both the proportion of autogenous females and the number of eggs was greater under

controlled conditions as larvae had access to a high protein diet in excess of their needs. In nature, winter temperatures were advantageous to the expression of autogeny but the larval diet would have been diminished, and lipoprotein reserves would have been lower. This is supported by the data on wing length (Tables 1, 2), which are a measure of body size/weight.

The Sydney population was 100% autogenous and laid equal numbers of eggs whether they were mated or not, and whether the adults were given a carbohydrate diet or only water. The results may have been different had the temperatures been 10°C higher, as lipoprotein reserves would have been considerably lower. Under such conditions, adults may well have required a carbohydrate diet. The lower rearing temperature and the longer development time at 16°C allowed for the accumulation of lipoproteins for maximum egg production in adults. Mating and a carbohydrate meal may have an effect in nature where the larval diet is nutritionally poorer, or under controlled conditions where larvae develop more rapidly (e.g. at a high rearing temperature), and as a result adults have fewer lipoprotein reserves (O'Meara and Krasnick 1970; Reisen *et al.* 1984).

Autogeny was common to all populations of *Ae. australis* examined from New South Wales, but it varied from 0-100% autogenous females from other regions of Australia (Table 4). Out of

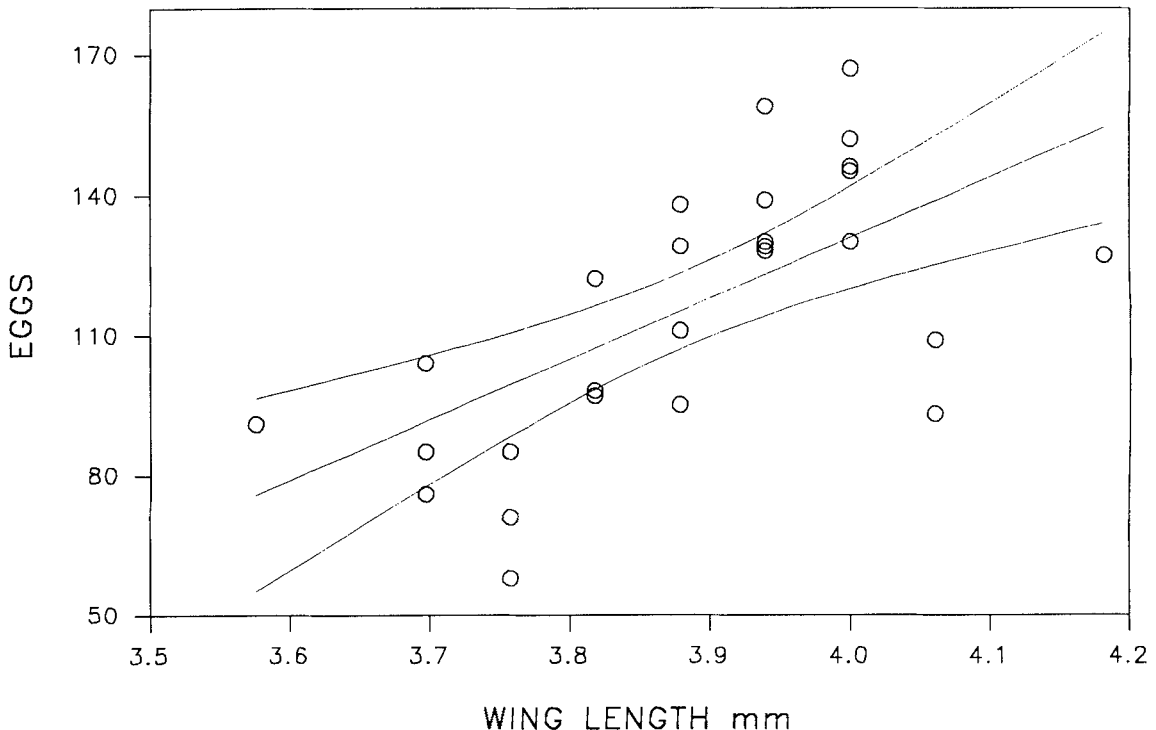


Fig. 2. Relationship between the number of autogenous eggs produced by females of a Durras, NSW population of *Ae. australis* and wing length. The straight line represents the regression and the curved lines represent the 95% Confidence Limit of the regression  $Y = -387.9 + 7.86X$  ( $R^2 = 0.39$ ,  $n = 29$ ,  $P < 0.002$ ).

five collections from coastal rock pools in Tasmania, only one collection had 100% autogenous females. The larvae and adults of all collections were reared under the conditions most favourable to the expression of autogeny, but autogeny was absent in females from two collections and there was a low expression of autogeny in females from the other two collections (Table 4). The Devonport and Low Head sites were 40 km apart and adults from these sites likely interbreed in nature and represent one population. Unlike females from the Devonport and Low Head collections which were anautogenous and had similar wing lengths, the Marrawah collection represents a different population as the females were significantly larger and were 100% autogenous. Marrawah is 150 km from Devonport, and from the lack of sharing of autogenous genes (O'Meara 1972), the adults evidently have not interbred in recent history. This could be a lack of conspecific recognition by adults from Marrawah and Devonport that keeps the populations from interbreeding or there may be a physical barrier that prevents adult dispersal. The winds off the western coast of Tasmania may be unfavourable for mosquito flight, and atmospheric conditions may keep these populations apart. Swansea and Kingston collections had similar proportions of autogenous females, and the adults were similar in size (Table 4). The adults from these sites likely interbreed, or have done so in recent history. Swansea and Kingston collections represent a third population, out of five collections in this study from Tasmania. The per cent autogenous females for Kingston is also similar to the population collected in Purakanui, NZ (Table 4). The possibility has been raised by Marks (in Nye 1962) and by Pillai and Ramalingan (1984) that the New Zealand population may have been transported by ship from Australia. If this hypothesis is true, it possibly originated from southeastern Tasmania. However, further studies are needed to test this hypothesis as well as a second hypothesis that the New Zealand population dispersed from other islands in the Pacific (Belkin 1968).

Autogeny in populations of *Ae. australis* was in part dependent upon latitude (Table 4), as has been shown in *Ae. togoi* (Sota 1994; Sota and Mogi 1995). In *Ae. togoi*, the proportion of autogenous females at 20°C and 10L:14D was greatest near the equator and was least at 49.2° North latitude (Sota and Mogi 1995). There were exceptions to this trend, as some southern populations were not fully autogenous, and some northern populations had 100% autogenous females (Sota and Mogi 1995). In the Southern Hemisphere, autogeny in *Ae. australis* was also higher in some populations closer to the equator (Table 4). There were exceptions to this trend, as Wardang Island is latitudinally north of the

Durras, Guerilla Bay and Marrawah sites, but the Wardang Island females were anautogenous while the others were autogenous.

Like *Ae. atropalpus* (Coquillett) (Hudson 1970), autogenous *Ae. australis* took blood when females were placed close to the host. The females did not use the blood to increase the number of eggs developed (Table 5), which is similar to what occurs in *Ae. atropalpus* (Hudson 1970). The results might have been different had the immatures of *Ae. australis* developed in the field where larval food resources were limited, and if rock pool temperatures were substantially higher than they were in the laboratory experiment. The number of autogenous eggs would have been less (Tables 1, 2), and the blood-meal may then have been used to begin vitellogenesis in undeveloped follicles, as occurs in *Ae. togoi* (McGinnis and Brust 1983). The low temperature and high protein larval diet favoured maximum autogenous development, and all the potential follicles had undoubtedly initiated vitellogenesis prior to the female taking blood.

The *Ae. australis* complex is probably distributed more widely in the Australasian Region than is currently recorded. Blood feeding populations are now known to be widespread, and humans are probably the most common host for these populations. Anautogenous populations occur in South Australia and Tasmania and the population from southeastern New Zealand was virtually anautogenous as well (Table 4). The literature is incomplete with regard to testing a number of different populations of *Ae. australis* for the ability of females to act as potential hosts for arboviruses. Females from eastern Tasmania and New Zealand may be better experimental hosts of Ross River virus (Austin and Maguire 1982; Kay and Aaskov 1989) than populations from New South Wales for example, where the females are autogenous. More populations in Australia should be evaluated for the ability of females to vector Ross River virus. The existence of anautogenous and autogenous populations in *Ae. australis* also allows the possibility of conducting biological crosses to investigate the genetics of autogeny. This could contribute to further understanding the evolution of the blood-feeding habit.

#### Acknowledgments

I thank Joanne Daly, Max Whitten and Paul Wellings, Entomology Division, CSIRO, Canberra, Australia for funding, facilities and technical support to conduct the study while I was on sabbatical leave from the University of Manitoba. I thank Keith Wardhaugh for equipment supplied by his laboratory, and I am grateful to Don Bliss for his technical help. I am grateful to Marilyn Geary and Richard Russell for mosquito collections from Maroubra, Sydney, NSW, to Mani Pillai for a collection from Purakanui Bay, NZ, and to Christian Sommer and Robin Bedding for collections from several sites in Tasmania. The financial support from the Natural Sciences and Engineering Research Council of Canada grant A2545 is gratefully acknowledged.

## References

- AUSTIN, F. J. and MAGUIRE, T. (1982). Ross River virus in the South-west Pacific. *In* Mackenzie, J. S. (1982). Viral diseases in South-east Asia and the Western Pacific. Academic Press: Sydney.
- BELKIN, J. N. (1968). Mosquito studies (Diptera: Culicidae) VII. The Culicidae of New Zealand. Contributions of the American Entomological Institute 3: 1-182.
- BRUST, R. A. (1991). Environmental regulation of autogeny in *Culex tarsalis* (Diptera: Culicidae) from Manitoba, Canada. *Journal of Medical Entomology* 28: 847-853.
- BRUST, R. A. and MAHON, R. J. (1997). The resurrection of *Aedes (Halaedes) ashworthi* Edwards 1921: Morphological characterisation and separation from its sibling *Aedes (Halaedes) australis* (Erichson) 1842 (Diptera: Culicidae). *Australian Journal of Entomology* 36: 129-136.
- DOBROTORSKY, N. V. (1966). Mosquitoes of Tasmania and Bass Strait islands. Proceedings of the Linnean Society of New South Wales 91: 121-146.
- EBERLE, M. W. and REISEN, W. K. (1986). Studies on autogeny in *Culex tarsalis*: 1. Selection and genetic experiments. *Journal of the American Mosquito Control Association* 2: 38-43.
- HARBACH, R. E. and KNIGHT, K. L. (1980). Taxonomists' glossary of mosquito anatomy. Plexus Publishing Incorporated: New Jersey.
- HUDSON, A. (1970). Factors affecting egg maturation and oviposition by autogenous *Aedes atropalpus* (Diptera: Culicidae). *Canadian Entomologist* 102: 939-949.
- KAY, B. H. and AASKOV, J. G. (1989). Ross River Virus (Epidemic Polyarthrititis). *In* Monath, T. P. (1989). The Arboviruses: Epidemiology and Ecology, 4: 93-112. CRC Press: Baton Rouge.
- LEE, D. J., HICKS, M. M., GRIFFITHS, M., RUSSELL, R. C. and MARKS, E. N. (1984). The Culicidae of the Australasian Region. Monograph Series. Entomology Monograph No. 2. 3: 1-257 (pp.19-29). Australian Government Publishing Service: Canberra.
- MCGINNIS, K. M. and BRUST, R. A. (1985). Oogenesis in a North American population of *Aedes (Finlaya) togoi* (Theobald) (Diptera: Culicidae). *Canadian Journal of Zoology* 63: 2168-2171.
- NYE, E. R. (1962). *Aedes (Pseudoskusea) australis* Erichson (Diptera: Culicidae) in New Zealand. Transactions of the Royal Society of New Zealand, Zoology 3: 33-34.
- O'MEARA, G. F. (1972). Polygenic regulation of fecundity in autogenous *Aedes atropalpus*. *Entomologia Experimentalis et Applicata* 15: 81-89.
- O'MEARA, G. F. and CRAIG, G. B. (1969). Monofactorial inheritance of autogeny in *Aedes atropalpus*. *Mosquito News* 29: 14-22.
- O'MEARA, G. F. and EVANS, D. G. (1976). The influence of mating on autogenous egg development in *Aedes taeniorhynchus*. *Journal of Insect Physiology* 22: 613-617.
- O'MEARA, G. F. and KRASNICK, G. J. (1970). Dietary and genetic control of the expression of autogenous reproduction of *Aedes atropalpus* (Coq) (Diptera: Culicidae). *Journal of Medical Entomology* 7: 328-334.
- O'MEARA, G. F. and PETERSEN, J. L. (1985). Effects of mating and sugar feeding on the expression of autogeny in crabhole mosquitoes of the genus *Deinocerites* (Diptera: Culicidae). *Journal of Medical Entomology* 22: 485-490.
- PILLAI, J. S. and RAMALINGAN, S. (1984). Recent introductions of some medically important Diptera in the Northwest, Central and South Pacific (including New Zealand), pp. 81-101. *In* Laird, M. Commerce and the spread of pests and disease vectors. Praeger Special Studies. Praeger Scientific: New York.
- REISEN, W. K. (1986). Studies on autogeny in *Culex tarsalis*: 2. Simulated diapause induction and termination in genetically autogenous females. *Journal of the American Mosquito Control Association* 2: 44-47.
- REISEN, W. K., MILBY, M. M. and BOCK, M. E. (1984). The effects of immature stress on selected events in the life history of *Culex tarsalis*. *Mosquito News* 44: 385-395.
- RUSSELL, R. C. (1993). Mosquitoes and mosquito-borne disease in southeastern Australia. A guide to the biology, relation to disease, surveillance, control and the identification of mosquitoes in Southeastern Australia. Department of Medical Entomology, Westmead Hospital; Westmead, and Department of Medicine, University of Sydney: Sydney.
- SIEGEL, J. P., NOVAK, R. J. and RUESINK, W. G. (1994). Relationship between wing length and dry weight of mosquitoes. *Journal of the American Mosquito Control Association* 10: 186-196.
- SOTA, T. (1994). Larval diapause, size, and autogeny in the mosquito *Aedes togoi* (Diptera: Culicidae). *Canadian Journal of Zoology* 72: 1462-1468.
- SOTA, T. and MOGI, M. (1995). Geographic variation in the expression of autogeny in *Aedes togoi* (Diptera: Culicidae) under different temperature and photoperiod conditions. *Journal of Medical Entomology* 32: 181-189.
- SPADONI, R. D., NELSON, R. L. and REEVES, W. C. (1974). Seasonal occurrence, egg production, and blood-feeding activity of autogenous *Culex tarsalis*. *Annals of the Entomological Society of America* 67: 895-902.

(Accepted 17 February 1997)