24 Egg development in Australian mayflies (Ephemeroptera)

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The effect of different water temperatures on the rate of egg development in species of Tasmanocaenis, Baetis *and* Austrophlebioides *from the headwaters of the River Murray, south-east Australia has been studied. Eggs collected from adults in the field were reared in the laboratory at constant temperatures between 5 and 30°C. There was a relationship, linear on logarithmic scales, between water temperature (T°C) and the length of the egg incubation period (Y days), expressed by the equation:* $Y = aT^{-b}$*, where a and b are constants. There was no significant difference between two species of* Austrophlebioides. *In all species no hatching took place at 5°C. Hatching success at 30°C varied with species. Otherwise hatching success was generally high (>70 per cent). The number of degree-days necessary for egg development decreased with increasing temperature. Eggs artificially fertilized in the laboratory had low (<10 per cent) hatching success. In the species studied so far there appear to be no major differences in the egg development patterns of Australian mayflies compared to those in other continents.*

Introduction

Many studies during the last decade have shown the influence of water temperature on life cycles and egg development among aquatic insects (e.g., Brittain 1982, 1990; Butler 1984; Humpesch 1984; Sweeney 1984). Temperature relationships of the egg stage are often crucial in determining a species' distribution both in terms of its response to environmental parameters and in relation to resource partitioning between closely related species (Elliott 1988; Lillehammer et al. 1989).

The present data form part of a study of the environmental effects of Dartmouth Dam in north-eastern Victoria, Australia. The main emphasis has been on the distribution and life cycles of the downstream macroinvertebrate fauna. Summer irrigation releases from the dam can reduce water temperatures in the Mitta Mitta

River by 10-15°C. Knowledge of the timing of the egg stage and the effect of changed temperatures on the duration of egg development are important in assessing the impact of such releases.

Data on egg development and the effect of temperature are now available from several European and North American mayfly species (see Brittain 1990). The only similar data from the Southern Hemisphere are Suter and Bishop's (1990) recent studies in South Australia and Brittain and Campbell's (1991) investigation of egg development in *Coloburiscoides.*

Materials and Methods

There are many species in the three genera investigated, but only a limited number of species have so far been formally described (Campbell 1988). The *Tasmanocaenis* species from station 104 is the River Murray caenid sp. C, designated by Suter (1989). The two species of *Austrophlebioides* from stations 101 and 102 are distinct, but are so far undescribed (I. Campbell, Monash University, personal communication). Similarly, the *Baetis* from stations 102 and 103 are different species and distinct from those described (I. Campbell, Monash University, personal communication).

Extruded egg masses were removed from female imagos collected in the field, mainly from light traps operated at dusk. In some cases eggs were extruded by female imagos during transport to the laboratory, while other egg masses were dissected from female imagos and fertilized artificially in the laboratory.

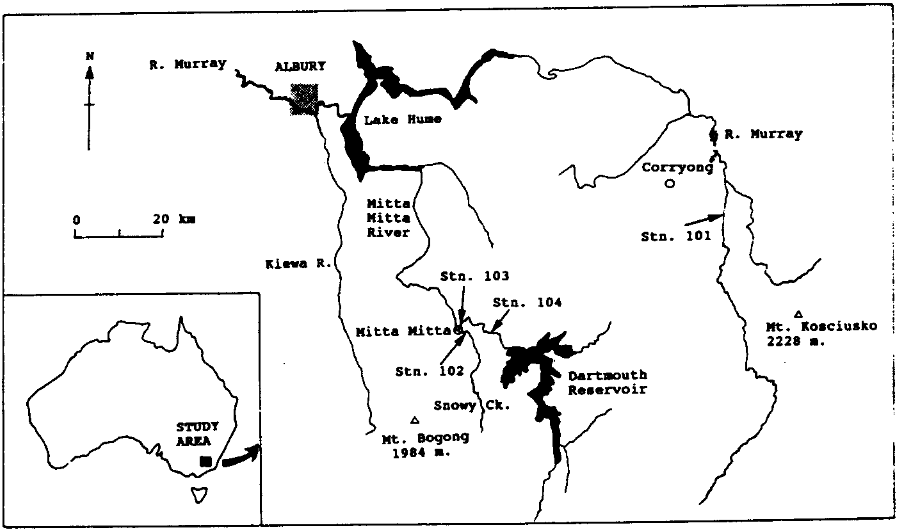
In the laboratory, the eggs in the masses were counted and placed in small Petri dishes at constant temperatures at 5°C intervals from 5°C to 30°C. The eggs at 20°C and 25°C were subject to normal day length, whereas the eggs at the remaining temperatures were kept in total darkness. There is no indication that photoperiod influences development time in mayfly eggs (Brittain 1982). This has been subsequently confirmed for Australian mayflies by Suter and Bishop (1991). The dishes were initially inspected twice weekly, but at the approach of hatching and after hatching had commenced they were inspected daily.

Field Sites

Field sites are located in north-east Victoria, on the headwaters of the River Murray (Fig. 1). All rivers rise in the Australian Alps at altitudes in excess of 1500 m a.s.l.

Site 101 is located at 280 m a.s.l. on the Murray River at Biggara (Indi Bridge) ca. six km before its confluence with the Swampy Plain River. The river is

Figure 1. Location of the collection sites in south-east Australia.



unregulated apart from minor water extraction. The flow is moderate and the substrate composed of stones and gravel.

Site 102 on Snowy Creek is situated at 270 m a.s.l., 200 m from the confluence with the Mitta Mitta River (site 4C in Doeg 1984), in a riffle area with cobble, stone and gravel substrate, downstream of a small dam. The creek has a natural flow regime.

Site 103 is situated on the regulated Mitta Mitta River at an altitude of 270 m a.s.l. and 200 m above its confluence with Snowy Creek at Mitta Mitta (site 4B in Doeg 1984). The flow is moderate and the substrate is composed of stones and gravel.

Site 104 is about eight km further up the regulated Mitta Mitta River towards Dartmouth Dam (site 2 in Doeg 1984) at 280 m a.s.l. The site is situated in a fast-flowing riffle area where the river flows through a narrow gorge. The substrate is largely composed of cobbles and stones, although there are areas of gravel in adjacent pool areas.

The macroinvertebrate fauna of the Mitta Mitta River and its tributary, Snowy Creek, have previously been investigated by Blyth et al. (1984) and Doeg (1984) in order to assess the impact of the construction of Dartmouth Dam and the initial irrigation release.

Results

Eggs of *Baetis* and *Austrophlebioides* were incubated at temperatures between 5° and 30°C. In both species hatching success was generally high (>70 per cent) in the range 10-25°C, while at 30°C only *Austrophlebioides* eggs hatched (Tables 1-3). The eggs of neither species hatched at 5°C. Certain eggs masses of *Austrophlebioides* showed low hatching success (<50 per cent). This appeared to be a function of egg mass rather than temperature. Hatching success was extremely low (0.4 per cent) for eggs of *Austrophlebioides* from station 103 artificially fertilized in the laboratory. At 30°C, hatching success was high in *Austrophlebioides*, but no eggs of *Baetis* hatched.

Eggs of *Tasmanocaenis* were only incubated at 10, 15 and 20 °C (Table 4). Hatching success was very high at both 15 and 20°C, but at 10°C no eggs hatched, although they appeared to be more or less fully developed with obvious eye-spots. Subsequent transfer of these eggs to higher temperatures (15, 20°C) did not induce hatching.

In *Baetis* and *Austrophlebioides*, there was a significant relationship, linear on logarithmic scales between water temperature (T°C) and the length of egg incubation (50 per cent hatch) (Y days), expressed by the equation: $Y=aT^{-b}$ (Table 5, Fig 2). The regressions for the two *Austrophlebioides* species were not significantly different.

Some data are also available for another *Baetis* sp. from the Mitta Mitta River at Mitta Mitta (Stn. 103). Incubation periods agreed well with the more extensive material from Snowy Creek.

When treated in the same manner, the limited data for *Tasmanocaenis* showed a similar relationship, and for comparative purposes, the values of the regression constants a and b were calculated to be 81552 and -2.95, respectively, although the regression analysis is obviously not statistically valid.

The number of degree-days required for egg development increased with falling temperatures. The increase in degree-day demand was especially noticeable in *Tasmanocaenis*. In all species, hatching was synchronous over the whole temperature range, 50 per cent of the eggs hatching within 1-4 days and 100 per cent within 1-20 days (Tables 1-4).

Discussion

The only data on the relationship between water temperature and the length of egg development in Australian mayflies are those of Suter and Bishop (1990) and

Table 1. **Egg development in *Austrophlebioides* from the River Murray at Indi Bridge (stn. 101). The number of days from oviposition to first hatch (Min.) and 50% hatch are given.**

Temp. °C	No.eggs	Date laid	Incubation period (d) Min.	50%	Hatch Duration	Degree-days, mean hatch	Hatch success (%)
5	1440	30.10.87	-	-	-	-	0.0
5	486	03.11.87	-	-	-	-	0.0
10	249	29.10.87	31	31	19	310	86.3
10	65	29.10.87	34	36	13	360	43.1
10	431	30.10.87	33	37	10	370	7.0
15	1006	29.10.87	22	22	8	330	73.9
20	578	29.10.87	12	12	9	240	36.7
20	1720	02.11.87	12	12	1	240	98.9
30	400	29.10.87	8	8	3	240	92.5
30	600	30.10.87	7	7	2	210	75.0

Table 2. **Egg development in *Austrophlebioides* from Snowy Creek (stn. 102). The number of days from oviposition to first hatch (Min.) and 50% hatch are given.**

Temp. °C	No.eggs	Date laid	Incubation period (d) Min.	50%	Hatch Duration	Degree-days, mean hatch	Hatch success (%)
5	285	23.01.88	-	-	-	-	0.0
10	414	22.01.88	-	-	-	-	0.0
10	680	28.10.87	35	35	9	350	2.4
15	891	23.01.88	20	21	17	315	3.9
20	31	22.01.88	11	11	2	220	32.3
25	376	23.01.88	7	8	11	200	4.3

Table 3. Egg development in *Baetis* from Snowy Creek (stn. 102). The number of days from oviposition to first hatch (Min.) and 50% hatch are given.

Temp. °C	No.eggs	Date laid	Incubation period (d) Min.	50%	Hatch Duration	Degree-days, mean hatch	Hatch success (%)
5	402	22.01.88	-	-	-	-	0.0
5	1187	23.01.88	61	61	-	(305)	0.1
5	182	24.02.88	-	-	-	-	0.0
10	651	22.01.88	25	26	14	260	40.9
10	1988	23.01.88	24	24	18	240	98.9
10	206	24.02.88	23	25	11	250	92.7
15	175	22.01.88	14	17	20	255	85.7
15	149	22.01.88	15	17	17	255	95.3
15	228	23.01.88	13	14	19	210	96.5
15	398	24.02.88	9	11	13	165	70.6
20	1105	23.01.88	7	8	17	160	98.2
20	721	24.02.88	9	11	20	220	85.6
20	161	22.01.88	7	7	6	140	3.1
25	262	23.01.88	4	5	9	125	90.5
25	98	24.02.88	5	5	5	125	89.8
30	823	24.02.88	-	-	-	-	0.0
30	567	24.02.88	-	-	-	-	0.0

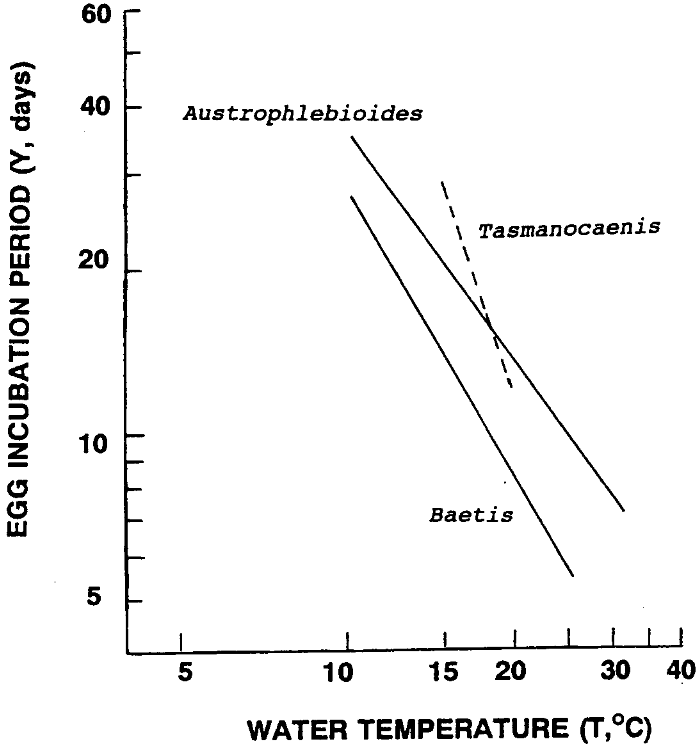
Table 4. Egg development in *Tasmanocaenis* from the Mitta Mitta River (stn. 104). The number of days from oviposition to first hatch (Min.) and 50% hatch are given.

Temp. °C	No.eggs	Date laid	Incubation period (d) Min.	50%	Hatch Duration	Degree-days, mean hatch	Hatch success (%)
10	404	14.12.87	-	-	-	-	0
15	238	14.12.87	26	28	14	420	98.3
20	390	14.12.87	12	12	2	240	98.7

Table 5. **Regression data for the relationship between length of egg incubation (Y days) and water temperature (T, °C) in *Austrophlebioides* spp. and *Baetis* sp. as expressed by the equation $Y=aT^{-b}$, where a and b are constants.**

Species	Station	n	a	b+S.E.	R^2	p
Austrophlebioides	Stn. 101	8	920	-1.423±0.077	0.98	<0.0001
Austrophlebioides	Stn. 102	4	1667	-1.657±0.140	0.99	<0.01
Baetis	Stn. 102	12	1365	-1.707±0.159	0.92	<0.0001

Figure 2. **Relationship between water temperature (T°C) and egg incubation period (Y days) in *Austrophlebioides* from the Murray River (stn. 101), *Baetis* from Snowy Creek (stn. 102) and *Tasmanocaenis* from the Mitta Mitta River (stn. 104), expressed by the regression equation: $Y = aT^{-b}$.**



Brittain and Campbell (1991). In most species, a significant power law relationship between water temperature and the length of egg development has been found. Regression constants in the present study were similar to those found in the cited Australian studies and also within the range found for northern hemisphere mayfly species (Brittain 1990).

Many Australian aquatic insects, particularly mayflies, appear to have less synchronous life histories that their European and North American counterparts (e.g., Hynes and Hynes 1975; Campbell 1986), although this may not be the case if equivalent latitudes and water temperatures are compared (Lake et al. 1988). Lack of synchrony is unlikely to be due to extended egg hatching, as synchronous hatching was found throughout this study, as well as in most of the Australian mayfly species so far studied (Campbell 1986; Suter and Bishop 1990; Brittain and Campbell 1991). However, Suter and Bishop (1990) did find a temperature induced quiescence in two South Australian species, whereby development was arrested at temperatures below 12-15°C. However, such quiescence has also been reported for European species (Brittain 1982).

Austrophlebioides and *Baetis* show similar temperature regressions, although the lower temperature limit for *Baetis* suggests that it is somewhat less warm adapted. The temperature-egg development characteristics are in fact very similar to the European *B. rhodani* (Elliott 1972). In contrast, the South Australian *B. soror* had much higher regression constants (Suter and Bishop 1990) and is clearly more warm adapted.

The data for *Tasmanocaenis* indicate a highly warm adapted species, and both thermal demand and temperature dependence (*sensu* Brittain 1990) are extremely high and akin to the North American *Hexagenia* (Friesen et al. 1979). Caenids are a major component of the Australian mayfly fauna, especially in the tropics, and a study of their egg development characteristics would be of considerable interest.

In terms of the relationship between water temperature and egg development as well as hatching synchrony, most Australian mayflies appear to have characteristics similar to their Northern Hemisphere relatives. However, few mayflies have been studied in tropical areas of the continent and such species may well display different temperature relationships in the egg stage in order to survive the high water temperatures and variable flows often encountered.

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References

Blyth, J.D., T.J. Doeg and R.M. St Clair. 1984. Response of the Mitta Mitta River, Victoria, to the construction and operation of Dartmouth Dam. 1. Construction and initial filling period. *Occas. Pap. Mus. Vict.* 1: 83-100.

Brittain, J.E. 1982. Biology of mayflies. *Annu. Rev. Entomol.* 27: 119-147.

Brittain, J.E. 1990. Life history strategies in Ephemeroptera and Plecoptera. P. 1-12 in I. Campbell (Ed.), *Mayflies and Stoneflies: Life Histories and Biology.* Dordrecht: Kluwer Academic Publishers.

Brittain, J.E. and I.C. Campbell. 1991. The effect of temperature on egg development in the Australian mayfly genus *Coloburiscoides* (Ephemeroptera: Coloburiscoidae) and its relationship to distribution and life history. *J. Biogeogr.* 18: 231-235.

Butler, M.G. 1984. Life histories of aquatic insects. P. 24-55 in V.H. Resh and D.M. Rosenberg (Eds.), *The Ecology of Aquatic Insects.* New York: Praeger.

Campbell, I.C. 1986. Life histories of some Australian siphlonurid and oligoneurid mayflies (Insecta: Ephemeroptera). *Austral. J. Mar. Freshwat. Res.* 37: 261-288.

Campbell, I.C. 1988. Ephemeroptera. *Zoological Catalogue of Australia* 6: 1-22.

Doeg, T. 1984. Response of the macroinvertebrate fauna of the Mitta Mitta River, Victoria, to the construction and operation of Dartmouth Dam. 2. Irrigation release. *Occas. Pap. Mus. Vict.* 1: 101-108.

Elliott, J.M. 1972. Effect of temperature on the time of hatching in *Baetis rhodani* (Ephemeroptera: Baetidae) *Oecologia* 9: 47-51.

Elliott, J.M. 1988. Egg hatching and resource partitioning in stoneflies (Plecoptera): ten British species in the family Nemouridae. *J. Anim. Ecol.* 57: 201-215.

Friesen, M.K., J.F. Flannagan and S.G. Lawrence. 1979. Effects of temperature and cold storage on development time and viability of eggs of the burrowing mayfly *Hexagenia rigida* (Ephemeroptera: Ephemeridae). *Can. Entomol.* 111: 665-673.

Humpesch, U.H. 1984. Egg development of non-diapausing exopterygote aquatic insects occurring in Europe. *Osterr. Akad. Wissench. Mat.-nat. Kl. Abt. 1.* 193: 329-341.

Hynes, H.B.N. and M.E. Hynes. 1975. The life histories of many of the stoneflies (Plecoptera) of south-eastern mainland Australia. *Austral. J. Mar. Freshwat. Res.* 26: 113-153.

Lake, P.S., L.A. Barmuta, A.J. Boulton, I.C. Campbell and R.M. St. Clair. 1985. Australian streams and northern hemisphere stream ecology: comparison and problems. *Proc. Ecol. Soc. Australia* 14: 61-82.

Lillehammer, A., J.E. Brittain, S.J. Saltveit and P.S. Nielsen. 1989. Egg development, nymphal growth and life cycle strategies in Plecoptera. *Holarct. Ecol.* 12: 1473-186.

Suter, P.J. 1989. Key to the mature caenid nymphs of the River Murray and other streams of south eastern Australia. Unpublished paper prepared for Ephemeroptera Taxonomy Workshop at the Murray-Darling Freshwater Research Centre, 14 February 1989.

Suter, P.J. and J.E. Bishop. 1990. Post oviposition development of eggs of South Australian mayflies. P. 85-94 in I. Campbell (Ed.), *Mayflies and Stoneflies: Life Histories and Biology.* Dordrecht: Kluwer Academic Publishers.

Sweeney, B.W. 1984. Factors influencing life-history patterns in aquatic insects. P. 56-100 in V.H. Resh and D.M. Rosenberg (Eds.), *The Ecology of Aquatic Insects.* New York: Praeger.