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The effect of temperature on egg development in the Australian mayfly genus *Coloburiscoides* (Ephemeroptera: Coloburiscidae) and its relationship to distribution and life history

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Abstract. The eggs of *Coloburiscoides* sp. (near *haleuticus*) were incubated in the laboratory at constant temperatures in 5°C intervals between 5°C and 30°C. There was a significant relationship between water temperature (T°C) and the length of the egg incubation period (Y days), expressed by the logarithmic equation: $Y=2217T^{-1.61}$ ($r^2=0.996$, $P<0.01$).

Hatching success was high (>80%) at temperatures between 10°C and 25°C. No eggs hatched either at 5°C or 30°C. The number of degree-days necessary for egg development decreased with increasing temperature. Eggs artificially fertilized in the laboratory had low (<10%) hatching success.

These results suggest that *Coloburiscoides* is warm adapted rather than cold adapted as previously thought, and suggest that its absence from Tasmania may be due to extinction during a recent glacial period. The low sychrony of life histories of Australian aquatic insects in lower altitude streams may be a response to higher temperatures rather than to hydrological variability.

Key words. Mayflies, temperature, eggs, distribution, life histories, Australia.

INTRODUCTION

Many studies during the last decade have shown the influence of water temperature on life cycles in general and egg development in particular among aquatic insects (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).

Our 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 reduce water temperatures in the River Mitta Mitta 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 the 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 is Suter & Bishop's (1990) recent work in South Australia. However, this does not include any representatives from the Coloburiscidae.

The mayfly family, Coloburiscidae, is endemic to the southern hemisphere, occurring in Australia, New Zealand and South America. The genus *Coloburiscoides* is widespread and abundant in upland stony streams in mainland southeastern Australia, but is surprisingly absent from the island of Tasmania despite the presence of suitable habitats (Campbell, 1981, Fig. 1).

MATERIALS AND METHODS

There are many species of *Coloburiscoides*, but only three species have so far been formally described (Campbell, 1988). The species in the present study is close to *C. haleuticus* (Eaton). A nymph and a male imago have been lodged in the National Museum of Victoria in Melbourne.

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.

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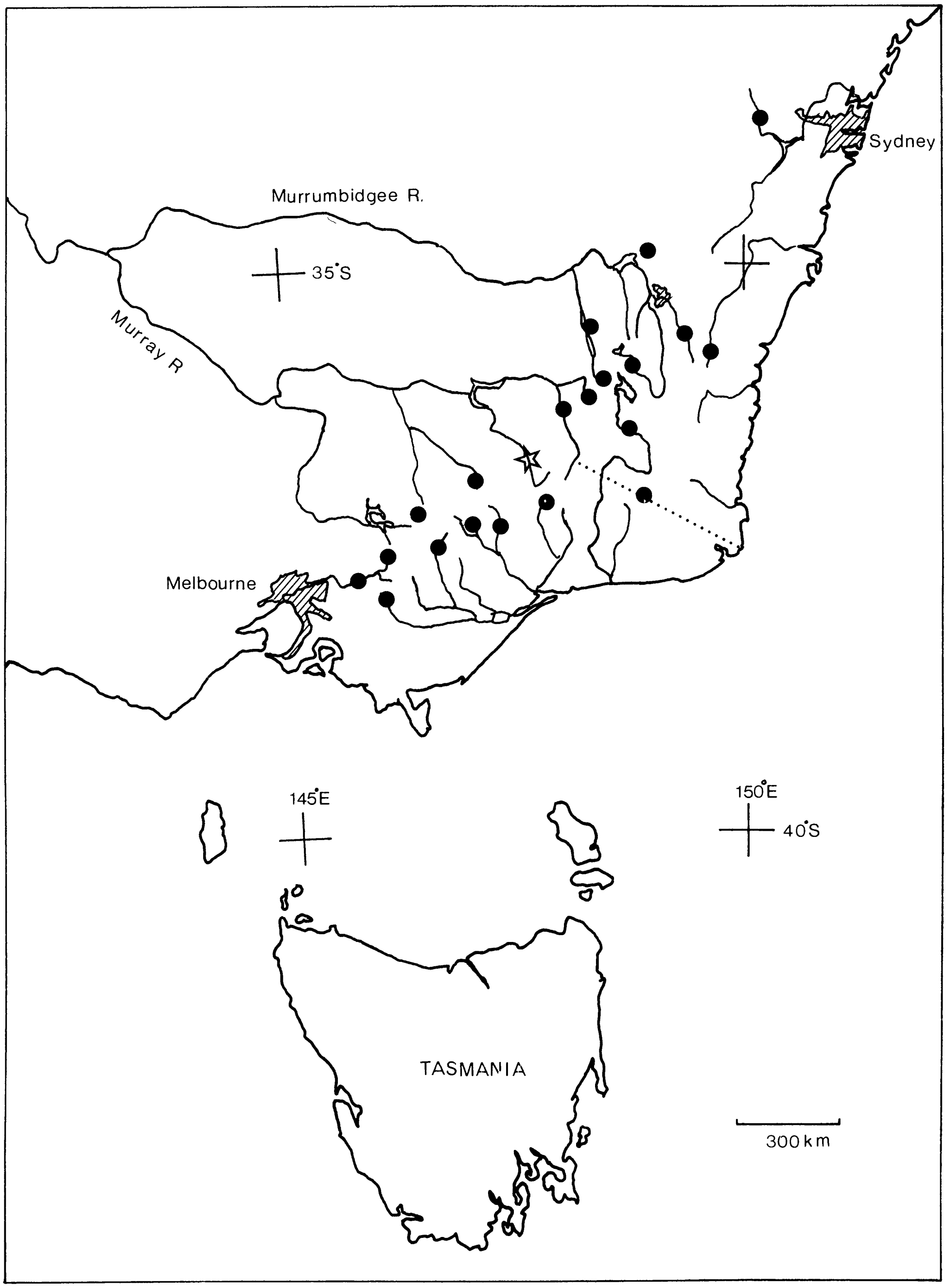

FIG. 1. Map of southeastern mainland Australia and Tasmania indicating the location of the study site (star) and other locations where *Coloburiscoides* is known to occur (solid circles).

In the laboratory, the eggs 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 daylength, 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). The dishes were initially inspected twice weekly, but at the approach of hatching and after hatching had commenced, they were inspected daily.

FIELD SITE

The field site is situated on Snowy Creek at Mitta Mitta in north-east Victoria, in the headwaters of the Murray-Darling catchment (Fig. 1). The site is 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 macroinvertebrate fauna of the Mitta Mitta River and its tributary, Snowy Creek, have previously been

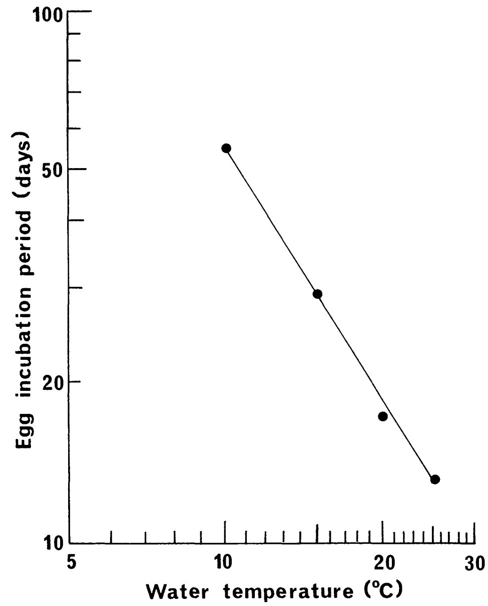

FIG. 2. Relationship between water temperature (T°C) and egg incubation period (Y days) in *Coloburiscoides*, expressed by the regression equation: Y=2217$T^{-1.61}$ (r^2=0.99, P<0.01).

investigated by Blyth, Doeg & St Clair (1984) and Doeg (1984) in order to assess the impact of the construction of Dartmouth Dam and the initial irrigation release.

RESULTS

Hatching success was high (>80%) in the temperature range 10–25°C for the fertilized eggs collected in the field (Table 1). However, both at 5°C and 30°C, no eggs hatched at all. Hatching success was low for eggs artifically fertilized in the laboratory, varying between 2% and 6% (Table 1).

Over the range 10–25°C there was a significant relationship for naturally fertilized eggs, linear on logarithmic scales between water temperature (T°C) and the length of egg incubation (50% hatch) (Y days), expressed by the equation: $Y=aT^{-b}$, where a=2217 and b=1.61±0.07 (SE). The proportion of the variance of Y due to its regression on T (r^2) was 0.99 (P<0.01) (Fig. 2). Although hatching success was low in the artificially fertilized eggs, the length of egg development showed a similar relationship to temperature over the range 10–20°C (a=1127, b=1.38±0.22, r^2=0.98), although the regression was not significant (P>0.05) due to the low number of egg batches.

The number of degree-days required for egg development increased with falling temperatures, from 325 degree-days at 25°C to 550 degree-days at 10°C. The increase in degree-day demand was especially noticeable at lower temperatures (Table 1). Hatching was synchronous at all temperatures, 50% of the eggs hatching within 1–2 days and 100% within 6–17 days (Table 1).

DISCUSSION

The only data on the relationship between water temperature and the length of egg development in Australian mayflies is that of Suter & Bishop (1990), who studied five South Australian species of Leptophlebiidae and Baetidae. In most species they found significant relationships (linear on logarithmic scales) between water temperature and the length of egg development. Regression constants were similar to that found for *Coloburiscoides* and for many northern hemisphere mayfly species (Brittain, 1990).

Eggs of *Coloburiscoides*, fertilized artificially in the laboratory, showed low hatching success compared to those fertilized in the field. It is possible, therefore, that few eggs were fertilized. In some Ephemeroptera fertilization is not required for development (Brittain, 1982), but this does not seem to be true for *Coloburiscoides*.

Campbell (1986) found that eggs of *Coloburiscoides* species, *munionga* (Tillyard) and an undescribed species erroneously referred to as *C. munionga* displayed synchronous hatching. He incubated eggs at 22–25°C, and found a highly synchronous hatch, spanning 24 h, 14 days after collection (hatch rate >95%). Together these data suggest that

TABLE 1. Egg development in *Coloburiscoides* from Snowy Creek reared at constant temperatures in the laboratory. Eggs in dishes 208–209 and 153–157 were from a single egg mass. Eggs in dishes 26–29 were obtained from two female imagos and artificially fertilized in the laboratory.

Dish no. (°C)	Water temp.	No. eggs	Date laid	Incubation period (days) First hatch	50% hatch	Hatching duration (days)	Degree days for 50% hatch	Hatching success (%)
208	5	635	24.2.88	–	–	–	–	0
153	5	427	24.1.88	–	–	–	–	0
154	10	794	"	54	55	17	550	84.0
155	15	283	"	28	29	6	435	87.6
156	20	498	"	15	17	11	340	93.6
157	25	1055	"	12	13	7	325	95.6
209	30	1267	24.2.88	–	–	–	–	0
26	10	2043	3.11.87	42	45	7	450	2.3
27	15	890	"	29	29	3	435	5.8
28	20	2513	"	17	17	5	340	4.8
29	30	2027	"	–	–	–	–	0

synchronous hatching is characteristic of the genus. The data also support the suggestion by Campbell (1986) that *Coloburiscoides giganteus* Tillyard in Digger's Creek, near Mt Kosciusko has an egg or early nymphal diapause. The data presented here would indicate an egg diapause or quiescence as more likely, in view of the fact that the threshold temperature for egg development lies between 5°C and 10°C and Digger's Creek is below that temperature for at least part of each day from late March onwards, before egg development would be complete.

The extent to which Australian streams conform to ecological models developed in Europe and North America has been much discussed (Lake *et al.*, 1985; Williams, 1989). Many Australian aquatic insects, particularly mayflies, appear to have less synchronous life histories than their European and North American counterparts (e.g. Hynes & Hynes, 1975; Campbell, 1986). This phenomenon is probably not due to asynchronous egg hatching, at least in *Coloburiscoides*.

Several environmental differences have been invoked to explain lack of synchrony in the life histories of Australian stream invertebrates. These include environmental variability, higher stream temperatures and hydrological variability (Hynes & Hynes, 1975; Smith & Williams, 1983; Marchant *et al.*, 1984; Campbell, 1986). Within the Australian mayflies, including *Coloburiscoides*, the most synchronous life histories occur in populations in high altitude alpine or subalpine streams (Campbell, 1986; Duncan, 1972). In contrast, populations at low altitude sites have poorly synchronized life histories. The high altitude streams are colder and more hydrologically regular (Campbell, Duncan & Swadling, 1990), but the strong sensitivity to temperature of *Coloburiscoides* suggests that the relationship between altitude and synchrony is a response to thermal rather than hydrological factors.

Our results may also explain the geographical distribution of *Coloburiscoides*. Nymphs require fast current for filter-feeding and cobbles or wood and tree roots for shelter. They are restricted to upland streams and southeastern mainland Australia, extending north to about 34° in the Blue Mountains (L. Benson, pers. comm.) (Fig. 1). This northward limitation, together with its presence in high altitude streams of the Snowy Mountains, led Campbell (1981) falsely to conclude that *Coloburidscoides* is cool adapted. Its absence from Tasmania, where there is abundant apparently suitable habitat, was particularly puzzling. Egg development is, however, restricted to temperatures ranging from a minimum of 5–10°C and a maximum of 25–30°C. A higher hatching success at 25° (96%) than at 10°C (84%), and a substantially higher degree-day demand at lower temperatures, suggests that the genus is warm adapted. This may explain its distribution. Presumably *Coloburiscoides* was eliminated from Tasmanian streams during the Pleistocene glaciations (Davies, 1974) or earlier. Recent land bridges between the mainland and Tasmania probably lacked the fast flowing stony streams which *Coloburiscoides* nymphs require. Their presence at altitudes up to 2000 m a.s.l. in the Snowy Mountains may relate to these streams having extensive shallow, slow-flowing unshaded pools, where summer water temperatures may exceed 25°C (I. Campbell, unpublished data).

The northern limit of *Coloburiscoides* may be due to the lethal effects of high temperature on the eggs, or, more probably, the thermal tolerances of the nymphs. Nymphs collected in Blue Mountains streams were all consistently smaller than those from southern localities. This is consistent with the thermal equilibrium hypothesis of Vannote & Sweeney (1980).

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