

## Life Spans of Two Species of Tropical Mayfly Nymph (Ephemeroptera) from Magela Creek, Northern Territory

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### Abstract

The nymphs of *Cloeon fluviatile* and a species of *Tasmanocoenis* were common in the shallows (< 1 m) of two billabongs in Magela Creek, Northern Territory. Monthly estimates of abundance and length frequency showed that growth and reproduction occurred continuously. Estimates of the ratio of annual production to mean biomass ( $P/B$ ) were calculated with the size-frequency method, using different values for nymphal life span; these estimates, when compared with  $P/B$  values predicted from the literature, suggested that the nymphs had a life span of about 1 month. Such a rapid life cycle is at least in part the result of the high mean temperature (30°C) in the shallows.

### Introduction

A survey of macroinvertebrates in billabongs along Magela Creek, Northern Territory (Marchant 1980), showed that the nymphs of two species of mayfly, *Cloeon fluviatile* Ulmer and a species of *Tasmanocoenis*, occurred commonly in the shallows. Specimens were collected at regular intervals throughout 1 year and data from them are used in this paper to derive estimates of the life spans of the nymphs. Generally, little information on the life histories of mayflies in the tropics is available. In contrast, this is a well-studied feature of such insects in temperate regions where it has been firmly established (Sweeney 1978; Macan 1979) that increasing temperature shortens the life span of the nymphs.

*C. fluviatile* occurs in New Guinea and has previously been collected in Australia from the Mitchell Plateau (W.A.), Flinders Ranges (S.A.), and Armidale (N.S.W.) (Suter 1980); it appears restricted to still or slow water as are most species of *Cloeon*. The species of *Tasmanocoenis* is unidentified, but is similar to *Tasmanocoenis tillyardi* which occurs widely in southern Australia (Suter 1980); it is most common in still water.

### Study Area

A general description and map of the creek and its billabongs have been given by Hart and McGregor (1980). Magela Creek (12°35'S., 132°52'E.) is a tributary of the East Alligator River about 250 km east of Darwin and only flows during the wet season (December-April). During the dry season, water is confined to billabongs along the creek. Water level in these billabongs fluctuates throughout the year, and during this study (March 1979-March 1980) highest levels occurred in February and March and lowest levels in early December.

Observations were made on *C. fluviatile* and *Tasmanocoenis* sp. in two billabongs: Goanna and Mudginberri. Goanna (1–3 m deep according to season) is on a tributary (Gulungul Creek) to Magela Creek, and Mudginberri (7–10 m deep according to season) is on the main channel of the creek. During the wet season, beds of macrophytes develop in the shallows of both billabongs, but these persist longer in Goanna than in Mudginberri; the shelving banks of the former billabong provide the shallow water necessary for these plants for a longer period than the steep banks of the latter billabong. During the study, the mean temperature in the shallows of both billabongs, based on monthly readings taken in the morning, was 30°C (range 24–38°C).

## Methods

Samples were taken monthly from the littoral region (< 1 m deep) of both billabongs, using a triangular hand net (30 cm wide) with 500- $\mu$ m mesh. Sweeps of 10 s duration were made at six sites to give a total sample of 1 min for each billabong. Each sweep vigorously disturbed any macrophytes present and the bottom debris which usually consisted of decaying leaves of *Pandanus aquaticus* F. Muell., *Barringtonia acutangula* Gaertn. and *Melaleuca* spp. overlying sand and silt. Samples were preserved in 90% ethanol within a few hours, after first being washed with water to remove larger debris. Nymphs were later sorted and counted and the body length ( $L$ ) measured (to the nearest 0.5 mm) under low magnification (6–8 $\times$ ). Both species appeared confined to the littoral zone as occasional samples taken in deeper water never contained nymphs. Nymphs and bred-out adults were deposited in the National Museum of Victoria.

Estimates of annual production ( $P$ ) and mean biomass ( $B$ ) were made with the size-frequency method (Hamilton 1969; Waters and Hokenstrom 1980). This method requires estimates of the mean weight of individuals. These were most conveniently provided by assuming that weight was proportional to the body length cubed ( $L^3$ ); Smock (1980) has shown for a variety of mayfly nymphs that it is in fact proportional to  $L^{2.9}$ .

## Results

Fig. 1 shows the monthly abundance of *C. fluviatile* and *Tasmanocoenis* sp. in the two billabongs; a logarithmic scale of abundance is used to display relative changes. In Goanna, greatest densities of both species occurred in the late wet season and early dry season (Fig. 1b). Densities declined after July and the species were apparently absent for about 2 months when water levels were at their lowest. Because water levels fluctuate, the extent of the littoral zone in this shallow, shelving billabong varies. Thus the samples do not necessarily represent a constant fraction of the population of nymphs present: during the wet season densities could be diluted as the nymphs colonize newly inundated areas, and during the dry season densities could be kept artificially high as the area of the littoral zone shrinks and the nymphs are crowded together. Despite these limitations, there were clear fluctuations in the abundances of both species between the wet season when densities and colonizable area were at a maximum and the dry season when both these factors were at a minimum. In Mudginberri, on the other hand, marked seasonal fluctuations were not evident and neither species disappeared when water levels were lowest (Fig. 1a). Again the counts from January to March perhaps do not reflect the size of the total population because during this period water flooded over the steep banks, inundating shallow areas. However, during the rest of the year, the littoral zone was confined to a narrow band below the top of the banks, and samples taken during this period probably represent a constant fraction of the total population of nymphs.

The length-frequency distributions of the two species from the monthly samples in both billabongs are shown in Table 1. It is evident that specimens of all sizes including

mature nymphs (as shown by dark or darkening wing pads) were present in nearly all months, indicating that growth, emergence and reproduction occurred continuously while the species were present. The smallest length classes were probably under-represented because some would not have been retained by the 500- $\mu\text{m}$  mesh and some would have been missed in the sorting. However, this does not alter the conclusion that both species develop continuously rather than in distinguishable cohorts.

Because cohorts are not distinguishable, it is not possible to estimate growth rates and nymphal life spans from Table 1. However, it is possible to estimate the nymphal life spans indirectly; this involves calculating the ratio of annual production to mean biomass ( $P/B$ ). As such calculations require a consistent index of population size (see above), data from Mudginberri between April and December were used. The fact that the smallest instars were under-represented in the samples should not affect the  $P/B$  ratio as the values for  $P$  and  $B$  will be lowered equally.

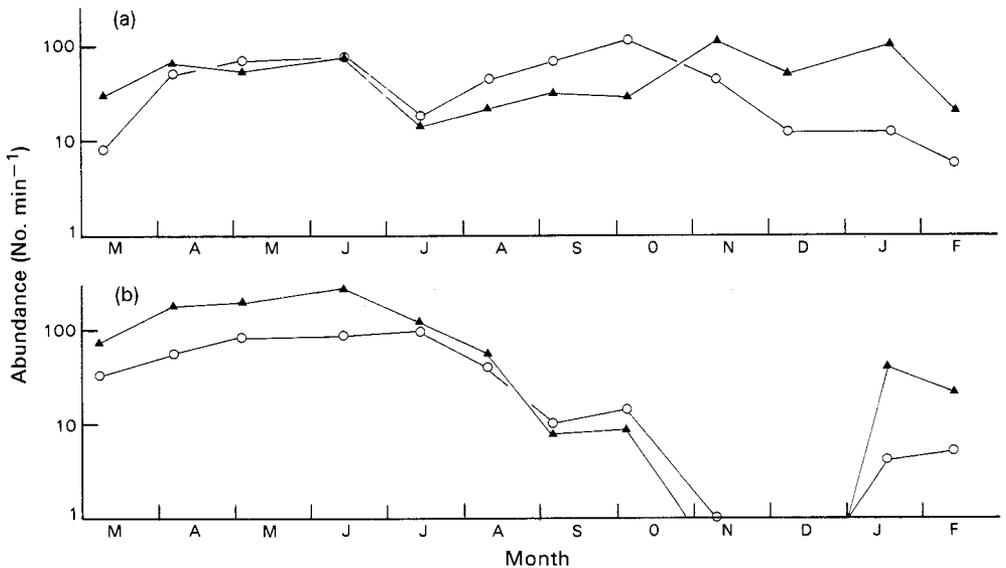


Fig. 1. Monthly abundances of *C. fluviatile* (▲) and *Tasmanocoenis* sp. (○) in Mudginberri (a) and Goanna (b) billabongs.

Annual production ( $P$ ) calculated with the size-frequency method assumes that the average size-frequency distribution is an estimate of the average cohort. This assumption is most likely to be true for populations with continuous recruitment and growth, as in these billabongs. The method has given reliable estimates of production for single species with yearly life cycles, including mayflies (Waters and Crawford 1973); and Benke (1979) has shown that it can be used with multivoltine insects provided an estimate of the nymphal life span is available. Thus, by using a variety of such estimates in the calculations and comparing the resultant  $P/B$  ratios with published data, the most likely nymphal life spans can be determined.

Table 2 gives the values of  $P$ ,  $B$  and  $P/B$  for both species for life cycles of 2, 4 and 8 weeks and indicates that the shorter the life cycle the higher the estimate of  $P$  and thus  $P/B$ . Banse and Mosher (1980) have analysed the  $P/B$  ratios from a large number of studies of aquatic and terrestrial invertebrates. They showed that at mean temperatures of 5–20°C about 85% of the variation in annual  $P/B$  was accounted for



by changes in adult size (given in kcalories). Studies conducted at higher temperatures ( $>25^{\circ}\text{C}$ ) had  $P/B$  ratios which were five times greater on average than those for an equivalent-sized animal at  $5\text{--}20^{\circ}\text{C}$ . By using equations given by Smock (1980) for Baetidae and Caenidae the lengths of mature *C. fluviatile* (5 mm) and *Tasmanocoenis* sp. (4 mm) can be converted to estimates of dry weight (mg) and then to kcalories [assuming 5 cal (21 J)  $\text{mg}^{-1}$  dry weight]. These estimates can be used in the equation given by Banse and Mosher (1980) to predict  $P/B$  from size, and the results can be multiplied by five to calculate the ratios at temperatures  $>25^{\circ}\text{C}$ . Thus, *C. fluviatile* should have a  $P/B$  of 28 and *Tasmanocoenis* sp. a  $P/B$  of 37. These predicted values are between those calculated for a 4-week and an 8-week life span of the nymphs (Table 2), although the value for *Tasmanocoenis* sp. is close to that given for a life cycle of 1 month. Waters and Crawford (1973) have shown that the size-frequency method slightly overestimates  $P$  and thus  $P/B$ . Therefore, it would be reasonable to conclude from these calculations that nymphs of both species have life spans of about 1 month.

**Table 2.** Indices of annual production ( $P$ ) and mean biomass ( $B$ ) for *C. fluviatile* and *Tasmanocoenis* sp., calculated with the size-frequency method

Subscripts indicate whether production is based on nymphal life spans of 2 weeks ( $P_2$ ), 4 weeks ( $P_4$ ) or 8 weeks ( $P_8$ ). Units are thousands of cubic millimetres per minute

Species	$B$	$P_2$	$P_2/B$	$P_4$	$P_4/B$	$P_8$	$P_8/B$
<i>C. fluviatile</i>	2.0	146.9	74	73.4	37	36.7	18
<i>Tasmanocoenis</i> sp.	1.2	101.8	85	50.9	42	25.5	21

The rapid resurgence of the populations of both species in Goanna at the beginning of the wet season is consistent with such short life cycles. The length-frequency distributions for 16 January 1980 (Table 1) show that a few nymphs of both species were close to emergence. Water levels rose rapidly about 2 weeks before this date, implying that these nymphs hatched from a resting stage and grew to maturity within this period. Gibbs (1973) found that *Cloeon triangulifer* in a pond in eastern Canada could survive the winter as diapausing eggs. It seems probable that both species in Goanna also produced such eggs in the late dry season, although it is possible that some nymphs survived, but at such low densities that they were not caught; and that when the billabong refilled these survivors were stimulated to emerge and reproduce.

## Discussion

The previous evidence indicates that, although the mean life span of nymphs of both species was about 4 weeks at an average  $30^{\circ}\text{C}$ , at certain times it may have been as short as 2 weeks. A limit to the length of the life span is set by some observations made by J. Martin (personal communication): while rearing chironomid larvae from billabongs along Magela Creek at a constant  $20^{\circ}\text{C}$ , he noted the emergence after about 2 months in culture of some *C. fluviatile* that were accidentally collected with the chironomids, presumably as eggs or very small nymphs. As already noted, monthly temperature readings in the shallows of the billabongs varied from  $24$  to  $38^{\circ}\text{C}$ , and for 9 months varied from only  $28$  to  $33^{\circ}\text{C}$ . Thus there seems little scope for low temperatures to increase life spans much beyond 4 weeks, especially considering Sweeney's (1978) demonstration that the developmental rates of mayfly nymphs are increased the more the temperature fluctuates diurnally. In both billabongs greatest diurnal fluctuations in

temperature occurred in the dry season when temperatures were lowest (Walker and Tyler 1979).

Oxygen levels are unlikely to affect the life spans of the nymphs. According to Walker and Tyler (1979), the shallows are well oxygenated, often reaching supersaturation when macrophytes are present. The factor that may have most influence on the life spans of nymphs in the field is food supply. As the littoral zone in Mudginberri varied less throughout the year than that in Goanna, it probably provided a steadier supply of food such as benthic algae and associated detritus and thus encouraged a more stable population of nymphs.

A nymphal life cycle of about 1 month is similar to those suggested by others who have studied aquatic insects in the tropics. In Uganda, Hynes and Williams (1962) found mature nymphs of a number of species of mayflies 1 month after they denuded a stream with DDT. Hynes (1975) concluded from a study of the seasonal changes of the insects of an intermittent stream in Ghana that the average life cycle was 2.5 months and noted that mature nymphs of the mayfly *Centroptilum* sp. were found only 18 days after resumption of flow in an intermittent tributary. The European species *Cloeon dipterum* has a summer generation that lasts approximately 2 months at water temperatures somewhat above 20°C (Cianciara 1979; Macan 1979).

From observations made while rearing mature nymphs, subimagos of both species emerge only at night. Edmunds and Edmunds (1980) suggest that exclusive nocturnal emergence of lowland tropical mayflies is an adaptation to escape heavy predation by insectivorous birds and Odonata during the day. Both of these are common along Magela Creek, especially the Odonata of which 64 species have been recorded (Watson 1980).

A light trap set up each month beside Goanna for 1 h at about 1900–2000 h seldom caught adults. This suggests that both species emerge soon after sunset (about 1800 h throughout the year) or later at night or that they do not swarm over the billabong. Edmunds and Edmunds (1980) recorded in Malaysia that Baetidae were the first to emerge at night, just before full darkness, and that after 1 h emergence of all families declined markedly; Caenidae emerged in the first hour of darkness or at dawn. Similar observations were made on the Ivory Coast by Elouard and Forge (1978). Edmunds and Edmunds (1980) also suggested that poor catches in Malaysia were probably due to swarming away from the nymphal habitat. During the first week of August 1979, large numbers of *C. fluviatile* and *Tasmanocoenis* sp. were attracted to lights in the Jabiru mining camp which was 1 km from the nearest billabong and about 2.5 km from Goanna. Smaller numbers were observed at these lights at other times, suggesting remote swarming was largely responsible for the low catches in the light trap.

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