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Food availability and life history patterns of aquatic insects in evergreen eucalypt forest streams in southeastern Australia

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Introduction

Life history patterns of many stream insects are thought to be influenced by the seasonal availability of food. ANDERSON & WALLACE (1984) suggest that evolution of life patterns to enable the exploitation of seasonally available foods has been a major factor generating the diverse patterns of life history currently present in aquatic insects. Often food availablity has been suggested as interacting with other environmental variables in structuring life history patterns. So, for example, MACKAY (1972) noted that differential responses to food and temperature formed the basis of niche partitioning for a group of 3 co-existing species of the shredding caddisfly *Pycnopsyche*, while HYNES (1970) suggested that the pattern of winter growth in many species of aquatic insects was a response to food availability resulting from autumnal leaf accession in deciduous forest streams together with reduced fish predation at lower water temperatures.

The prevailing paradigms on life histories of aquatic insects are derived almost exclusively from studies carried out in Europe and northern North America. These areas are characterized by cool temperatures, regular climates, frequently a deciduous vegetation and comparatively recent glaciation history. Much of the planet, and particularly Australia, is not so characterized (e. g. see WILLIAMS 1988), and as yet it is unclear to what extent the life history patterns of aquatic insects on which the paradigms are based are globally applicable.

Life history patterns of insects in southeastern Australian streams

LAKE et al. (1985) suggested that, contrary to the patterns found in many northern hemisphere stream insects, many, but not all, aquatic insects in southeastern Australian streams displayed life histories which were poorly synchronised with long emergence periods. Data published since that paper confirm their view.

In the Ephemeroptera, and particularly in the Leptophlebiidae, the total size range of nymphs is often present virtually throughout the year in southeastern Australian streams. These patterns have been demonstrated for a number of common leptophlebiid genera such as *Austrophlebioides* (Fig. 1) (CAMPBELL et al. 1990), *Kirrara* (CAMPBELL & HOLT 1984), *Atalophlebia* (SUTER 1980) as well as for genera in several other families (CAMPBELL 1986). At higher altitudes the life histories become substantially more synchronous with obvious cohorts apparent (CAMPBELL 1985, DUNCAN 1972).

In southeastern Australian Plecoptera, similar life history patterns are also often evident. For example, the occur in many of the Gripopterygidae, including species of *Riekoperla, Illiesoperla* and *Dinotoperla* (HYNES & HYNES 1975, YULE 1985).

Less data are available for southeastern Australian Trichoptera. Of the 9 species investigated by DEAN & CARTWRIGHT (1987), 6 showed poorly synchronised life histories with a wide size range of larvae present throughout the year. Three species, *Agapetus kimminsi*, *Hydrobiosella waddama* and *Chimarra monticola*, were more synchronous and were apparently absent from the stream as larvae for 2 or more months each year. None of the 5 species of stream dwelling Leptoceridae investigated by ST CLAIR (1993) displayed highly synchronous life histories.

These patterns seem to contrast with the life history patterns described for many aquatic insects in the northern United States, Canada and Europe. In those areas, life histories appear generally to be far more synchronous, with well defined cohorts present and far briefer adult emergence periods. For example several cases have been described of congeneric species coexisting with their life histories out of phase (e. g. HYNES 1976, MACKAY & WIGGINS 1979, WARD & STANFORD 1982), a situation which would not be possible for genera such as

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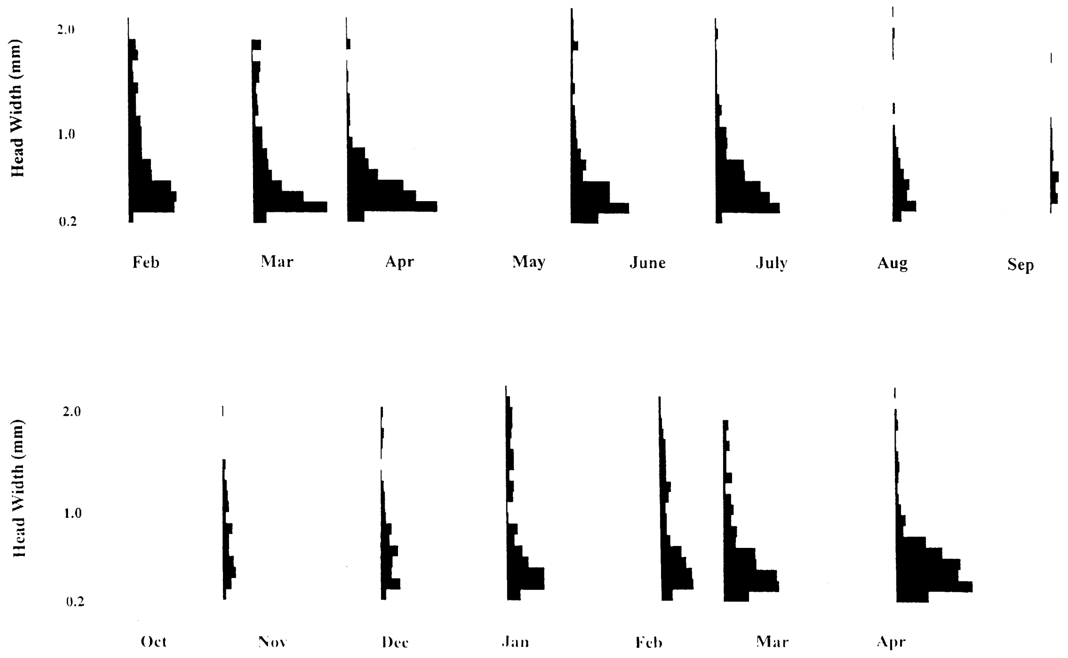

Fig. 1. Size frequency distributions for the leptophlebiid mayfly *Austrophlebioides* sp. 3 at monthly intervals during 1993–1994 in the Loch River, Victoria, Australia.

Austrophlebioides in southeastern Australia (Fig. 1). Similarly, many stream shredders in northern North American streams appear to have their life histories timed so that active larvae are absent from the stream during periods when food resources are scarce (Cummins 1964). This pattern does not appear to occur in Australian shredding insects.

Possible causal factors

Attribution of causal factors for synchrony or lack of synchrony depends on the ancestral state. If the ancestral state was a synchronous life cycle then we must seek for a cause of asynchrony in Australian populations. If on the other hand asynchronous life cycles were the ancestral state then factors causing synchrony in northern North America should be sought, but the lack of those factors in southeastern Australia would facilitate the asynchronous state.

A number of potential causal factors has been suggested as influencing the lack of synchrony in the life histories of Australian aquatic insects. Major potential factors include the greater hydrological variability (and reduced predictability) of Australian streams compared with those in North America, the reduced seasonality of available food and higher water temperatures.

Although it has often been suggested that higher water temperature is associated with reduced life history synchrony in aquatic insects, the suggestion has been difficult to prove. Higher water temperature could permit year round growth and a longer emergence period for adults. Both growth diapause and synchronous recruitment have been suggested as mechanisms for reinforcing life history synchrony. An analysis of published data by Clifford (1982) attempted to relate voltinism in mayflies with latitude. He suggested that multivoltinism should become increasingly common closer to the tropics, but confounding factors such as altitude prevented any simple pattern from being obvious from the data.

Marchant et al. (1984) have argued that the variability and/or unpredictability of the discharge patterns in Australian streams necessitate a flexible asynchronous life history. Spates may occur at any time of year, and droughts may be quite extended. Small larvae may avoid both by penetrating deep into the hyporheic, and adult insects avoid spates by surviving outside the stream. The value of adults as an avoidance strategy to bypass instream disturbance would be rather limited in the Ephemeroptera with their short adult life, but would be greater in the Trichoptera and Plecoptera. In this scenario it may be advantageous to have small larvae present virtually throughout the year, and this would constitute a positive pressure for an asynchronous life history.

Attempts to test this hypothesis have not been successful. MARCHANT et al. (1984) concluded that common indices of unpredictability were insufficiently sensitive to be useful for such a test. ST CLAIR (1993) found no evidence for reduced life history synchrony in populations of Trichoptera in an intermittent stream than in a permanent stream, although the intermittent stream was presumably more hydrologically variable.

Food as a facilitating factor

The final factor commonly linked to low life history synchrony is food availability. WILLIAMS & WAN (1972) first suggested that, since terrestrial leaves are an important source of food for stream invertebrates, and since southeastern Australian streams flow through evergreen forests, the supply of leaf material should be non-seasonal, whereas the supply of leaves in deciduous forest streams is decidedly seasonal. Recent data indicate that, although the supply of leaves to Australian forest streams is more seasonal than WILLIAMS & WAN (1972) suspected, it is less seasonal than is the case for deciduous forest streams (Table 1). Both eucalypt and deciduous forest streams receive similar amounts of terrestrial plant litter annually – 500–700 gm. m^{-2}. However the proportion of the annual leaf accession load entering the stream in the season of least accession (winter in both deciduous and eucalypt forests) is about 15 % for eucalypt forest and only about 5 % for deciduous forest streams (CAMPBELL & FUCHSHUBER 1994). Furthermore the proportion of the more nutritionally rich green leaves to abscissed leaves falling into eucalypt forest streams increases from about 15 % in summer to about 80 % in winter (CAMPBELL & FUCHSHUBER 1994). So the seasonality of food availability from terrestrial plant litter is substantially reduced in eucalypt *vs* deciduous forest streams.

Table 1. Proportion of the annual terrestrial litter accession reaching southeastern Australian eucalypt forest streams and Northern Hemisphere deciduous forest streams in each season. Each season is considered to consist of 3 calendar months with the southern hemisphere summer and the northern hemisphere winter consisting of December, January and February. Based on data from CAMPBELL et al. (1992).

Location	Summer (%)	Fall (%)	Winter (%)	Spring (%)	n
Australia	45	21	14	20	6
Northern Hemisphere	12	68	5	10	6

Patterns of terrestrial litter accession would therefore tend to favour the development of synchronous life histories synchronised with leaf fall in shredding invertebrates living in deciduous forest streams. Why such synchronous patterns should also occur in scraping invertebrates is less clear. One possibility is that the DOM pulse from leachates from terrestrial leaves is a synchronising factor. Alternatively the annual pulse of light and shade due to leaf out in deciduous forests may cause a resulting pulse in epilithic algal biomass.

Most headwater streams in southeastern Australia are groundwater fed rather than spring fed. The construction of an organic matter budget for one such stream, Keppel Creek, indicates that the overwhelming source of organic matter is dissolved organic matter (DOM) derived from groundwater (Table 2). There is no reason to believe that the accession of this material is strongly pulsed, and if there is a seasonal maximum it would be expected to occur in winter-spring, the season of highest rainfall, which would tend to counterbalance the pulse in DOM leaching from leaves, which mainly enter the stream in summer-autumn.

Thus, food availability for scraping invertebrates should be even less seasonal in south-

Table 2. Annual dissolved organic carbon accession to Keppel Creek expressed as $gm \cdot m^{-2} \cdot yr^{-1}$.

Terrestrial litter	745	(10 %)
Primary production	1,056	(14 %)
Groundwater	5,507	(75 %)
Total	7,308	

eastern Australian eucalypt forest streams than is the case for shredding invertebrates.

Conclusions

The absence of a pulsed food availability may facilitate asynchronous life histories in aquatic insects in southeastern Australian eucalypt forest streams. In contrast the strongly pulsed nature of food availability in deciduous forest streams may have forced the development of strongly synchronous and synchronised life histories in aquatic insects living there.

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