

Life history patterns of six sympatric species of Leptophlebiidae (Ephemeroptera) in a New Zealand stream and the role of interspecific competition in their evolution

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Abstract

Nymphal life histories of six sympatric species of Leptophlebiidae (Ephemeroptera) were studied in Waitakere River and its tributary, Cascade Stream, a kauri forest stream system in northern New Zealand. Species examined were *Neozephlebia scita* (Walker), *Austroclima jollyae* Towns & Peters, *Deleatidium myzobranchia* Phillips, *D. lillii* Eaton, *Deleatidium* sp. A and *Deleatidium* sp. C. A mixture of well and poorly synchronised life cycles occurred within the guild. Species of *Deleatidium* had life histories which ranged from univoltine (*D. lillii* and *D. myzobranchia*) to weakly bivoltine with overlapping generations and cohorts (*Deleatidium* sp. C). There was little evidence of temporal segregation, but instead a high degree of habitat and life history overlap. This conflicts with models based on stream insects from temperate northern hemisphere streams and usually attributed to niche differentiation in response to interspecific competition. The possible role of interspecific competition in evolution of life histories of stream invertebrates is assessed. It is noted that temporal segregation of life histories does not by itself demonstrate differential use of common resources by congeners, and that there is little direct evidence to support the widespread assumption that competition is a major influence on the evolution and composition of lotic communities.

Introduction

Recent ecological studies of stream invertebrates in New Zealand have shown a predominance of species with poorly synchronised life histories (Winterbourn 1978; Towns 1981a), including non-seasonal or weakly seasonal development patterns and long hatching and emergence periods. Even in cool, high altitude streams, there is little tendency towards synchronised seasonal life histories, although these might be expected according to the Hynes (1970) model of life history patterns (cf. Towns 1981a).

New Zealand leptophlebiid mayflies appear to have particularly unclear life histories, but most available data are clouded by uncertainty over specific identification or the number of species present. This raises the possibility that unclear life history

patterns found by Winterbourn (1974, 1978), Hopkins (1976) and Towns (1981a) for members of the family were an artifact of overlapping and seasonally staggered development periods of sympatric species. Staggered hatching and development periods in congeneric species have been shown for several temperate northern hemisphere groups, including mayflies (e.g. Grant & Mackay 1969; Wise 1980). This has commonly prompted the suggestion that some resource, probably food, is limiting during larval growth, and that selective forces have brought about temporal (or niche) separation which effectively acts to minimise interspecific competition (e.g. Kolding & Fenchel 1979).

The possibility of temporal segregation of New Zealand mayflies is investigated in this paper, which describes the nymphal life histories of six sympatric species of Leptophlebiidae as part of a

study of invertebrate communities in the Waitakere River, a stream in northern New Zealand mixed broadleaf-podocarp and kauri forest (Towns 1976, 1978a, 1978b, 1979, 1981a, 1981b). On the basis of results presented here, the possible role of interspecific competition in the evolution of life histories of sympatric species of stream invertebrates is assessed.

Leptophlebiid mayflies commonly dominate the benthic fauna of relatively undisturbed streams in New Zealand, and a large number of species may co-occur in the same catchment area (e.g. Towns 1978a). Because of taxonomic problems, previous life history studies have either assumed the presence (or dominance) of one species or attempted to restrict the analysis to a single phenotype (Winterbourn 1974, 1978, Hopkins 1976, Towns 1981a). The present investigation stems from my earlier study in which problems of species identity became apparent (Towns 1981a) and involves a separate sampling programme in a wider range of habitats. It is the first account of the life histories of a guild of New Zealand leptophlebiid mayflies which overlap in range and which can be identified to species throughout their nymphal life.

Study area

The Waitakere River (36°28'S, 174°31'E) drains a 34 km² watershed on the west coast of the northern North Island of New Zealand. In the upper half of its catchment the stream flows through relatively untouched mixed broadleaf-podocarp forest with large mature or regenerating stands of kauri (*Agathis australis* Salisb.); in the lower catchment it flows through stock-grazed scrub, regenerating forest and open, farmed areas.

Three sites were sampled in the forested section of the catchment near the confluence of the Waitakere River and one of its main tributaries, Cascade Stream. These included a riffle in the Waitakere River about 300 m downstream of Cascade Stream (site III of Towns 1979, 1981a), which will be referred to as the Waitakere River riffle, and two sites in Cascade Stream. One was a riffle immediately upstream of the confluence with the Waitakere River (site 'r' of Towns 1979) and the second was a cascade 10 m upstream of the riffle.

The two riffles differed slightly in structure, nor-

Table 1. Physical characteristics of the Cascade Stream and Waitakere River riffles during winter (July) and summer (February), from 3 to 5 measurements along a cross-sectional transect.

	Width (m)	Depth (cm)	Mean flow rate (m · sec ⁻¹)	Annual temperature range (°C)
Cascade				
July	4.3	8–14.5	0.27	8.5–16.1
February	2.7	5–13	0.38	
Waitakere				
July	6.2	10–23	0.28	8.5–17.0
February	5.3	4–34	0.11	

mal flow rate (Table 1) and composition of the substratum. The Waitakere River site consisted of cobbles and some boulders, whereas the Cascade Stream riffle was formed from pebbles, cobbles and numerous boulders. Daytime spot water temperatures in the two streams showed no difference during winter and spring, but during summer Cascade Stream was up to 1.4 °C cooler than Waitakere River (see also Table 1).

The cascade formed the downstream section of a complex series of narrow channels, cascades, waterfalls, riffles and pools, and had a substratum of solid conglomerate over which water flow rate was normally 0.5–1.9 m sec⁻¹.

Visible periphyton growths did not occur in the Cascade Stream riffle but were present in the Waitakere River site and on the cascade during spring and summer. Dominant algal genera were *Melosira* and *Oedogonium* on the cascade, and *Cladophora*, *Melosira*, *Spirogyra* and *Rhoicosphenia* in the Waitakere River riffle.

Additional information on the stream catchment and physicochemical characteristics of the waters is given in Towns (1979).

Methods and materials

Species identification

The species studied were *Deleatidium myzobranchia* Phillips, *Deleatidium* sp. A, *Deleatidium* sp. C, *Deleatidium lillii* Eaton, *Neozephlebia scita* (Walker) and *Austroclima jollyae* Towns & Peters.

All species were abundant in the vicinity of the Waitakere River–Cascade Stream confluence, but there were some distribution differences according to habitat; *Deleatidium myzobranchia* and *Austroclima jollyae* were mainly restricted to the cascade, whereas all other species were abundant in riffles. The two riffles were chosen as study sites after a pilot survey indicated that *Deleatidium* sp. A was the most abundant mayfly in the lower Cascade Stream, but *D. lillii* was more abundant in the Waitakere River, thus providing contrasting situations of species abundance. This supplemented an earlier study of longitudinal zonation which indicated distributional overlap of *Deleatidium* sp. A, *D. lillii*, and *Deleatidium* sp. C (Towns 1979).

Taxonomic nomenclature used here is based on Towns & Peters (1979) and Towns (1982). Nymphs of *Deleatidium* cannot be identified to species from Phillips' (1930) revision of the genus. Identity of the species discussed here was therefore based on rearing of nymphs to the adult, comparison of adults with original descriptions and material used by Phillips, and collection, rearing and association of all life stages from the vicinity of the species' type localities.

The four *Deleatidium* species represent two species in the '*myzobranchia*' group (gills with the apex rounded) and two in the '*lillii*' group (gills with the apex pointed) (Winterbourn 1978). *Deleatidium* sp. C is related to *D. lillii*, but most closely resembles *D. fumosum* Phillips. *Deleatidium* sp. A appears to be an undescribed species most closely related to *D. myzobranchia*. Each of the *Deleatidium* species could be distinguished throughout their nymphal life by abdominal colour pattern and pigmentation pattern of the thoracic and abdominal ganglia, but gill shape changed during growth and was only useful in distinguishing mature individuals.

Sampling

Samples were obtained monthly from March 1975 to March 1976 by stirring the substratum of riffles or sweeping the cascade rock surface into a 30 × 30 cm net with 200 µm mesh. Each area was sampled for about 5 min. Samples were preserved in 10% formalin and sorted in the laboratory under 10× magnification.

Analysis

Few of the species showed monthly size frequency distributions which could be interpreted visually, so size cohorts were identified by probability paper analysis (Cassie 1954). For each species several cohorts often overlapped in any one month. In these situations the break between cohorts was approximated as the middle of each point of inflection of the probability curve.

Difficulties presented by the Cassie method were discussed by Fink (1980), who mentioned the particular problem of identifying points of inflection. However, I found that it offered a more consistent and objective method of estimating ranges of component distributions than visual estimation from size frequency analyses. Cohort range was estimated by eye only where small numbers of specimens were obtained (<20).

For each cohort, the mean, standard deviation and proportion of the total population they represented were calculated.

Potential emergence was estimated from the presence of specimens with wing-pads >1.6 mm long. These were either black or large enough to enable emergence in the laboratory in less than one week at 15 °C. Specimens in this category are referred to below as 'mature nymphs', which represented the final one or two instars. Rearing methods used are outlined in Towns (1976).

Results

Neozephlebia scita

This species probably has two generations, although one, a summer hatching (January–February) generation predominates (Fig. 1). This generation grows relatively slowly over winter to emerge as adults the following spring and early summer – a nymphal life span of 8–11 months. A second, weaker generation hatches in winter and spring with some rapidly growing members merging with the winter generation, thus leading to apparent shrinking of the size range of some cohorts (e.g. December, Fig. 1). The second, small emergence of adults in late summer apparently results from this faster growing summer generation which has a nymphal life of 6–9 months. Because of this pattern, *N. scita* has a very

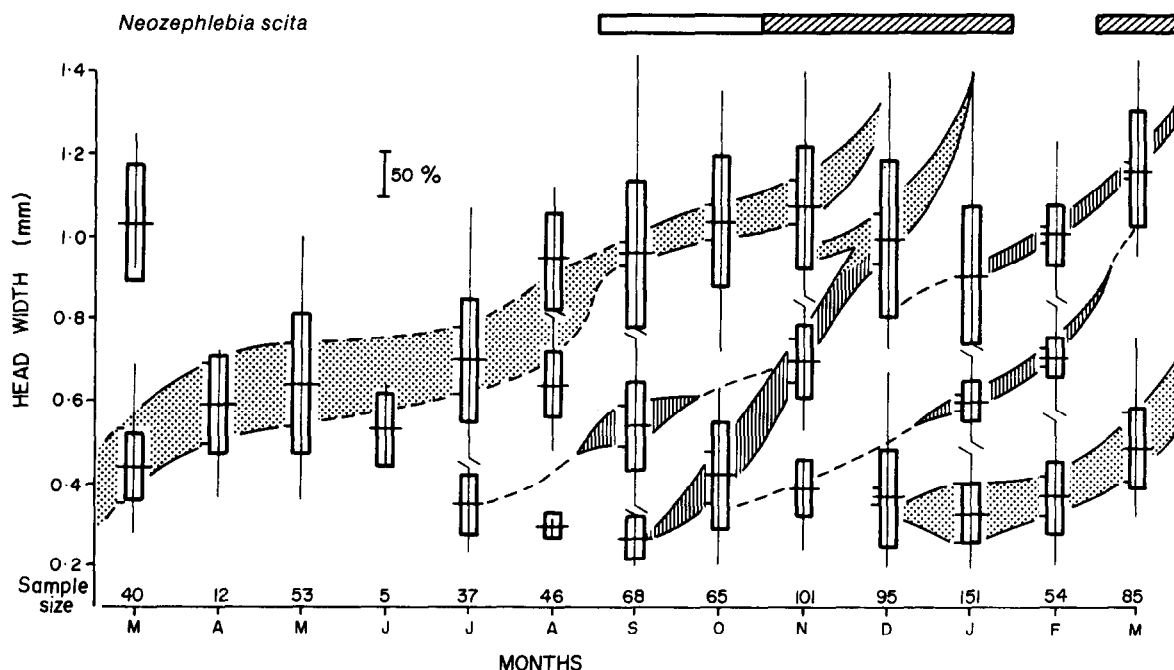


Fig. 1. Seasonal size distribution of *Neozephlebia scita*. Vertical lines, range; rectangles, standard deviation; horizontal lines, mean; lines joining cohorts represent possible generations, width proportional to contribution of cohort to monthly population (scale 50%); winter generation stippled, summer generation shaded; horizontal bar, nymphs with enlarged (unshaded) or black (shaded) wingpads (broken line, enlarged pads present but rare).

long hatching and emergence period. The latter is supported by light trap records from the Waitakere River catchment, which indicate a flight period of October–April (Towns 1982).

In a separate sampling programme in which specimens were grouped by size classes, I was unable to present a clear picture of the nymphal growth pattern of this species (Towns 1981a). The present analysis supports my previous suggestion of two emergence cohorts (generations) per year dominated by a winter generation.

Austroclima jollyae

The monthly size frequency distribution of this species shows no clear growth pattern, and division of the population into cohorts provides little added clarification (Fig. 2). This analysis does suggest that the species has constant recruitment of early instars and a very long potential emergence period. In all months the smallest size cohort represented the lowest proportion of the population, but this group was not located in other biotopes. Apparently *A. jollyae* is rare in most areas, but later instars con-

gregate in rapid flow environments to complete their nymphal life history.

Deleatidium lillii

This was one of the most abundant invertebrate species in forested sections of the Waitakere River (see Towns 1979, 1981a). Like *Deleatidium* sp. C, *D. lillii* was most common in riffle areas (Fig. 3), where it had a highly seasonal distribution. This seasonal abundance was reflected in the life history which consisted of a mass hatching in December and January, relatively slow growth (and a decline in numbers) and emergence in late summer early spring, after a nymphal life of 8–9 months (Fig. 4). There was also some evidence of a weak summer generation (Fig. 4), but these are more likely to represent slower growing individuals from cool tributary populations, as suggested by comparison of size distribution of summer samples from the Waitakere River and cooler Cascade Stream (Fig. 5).

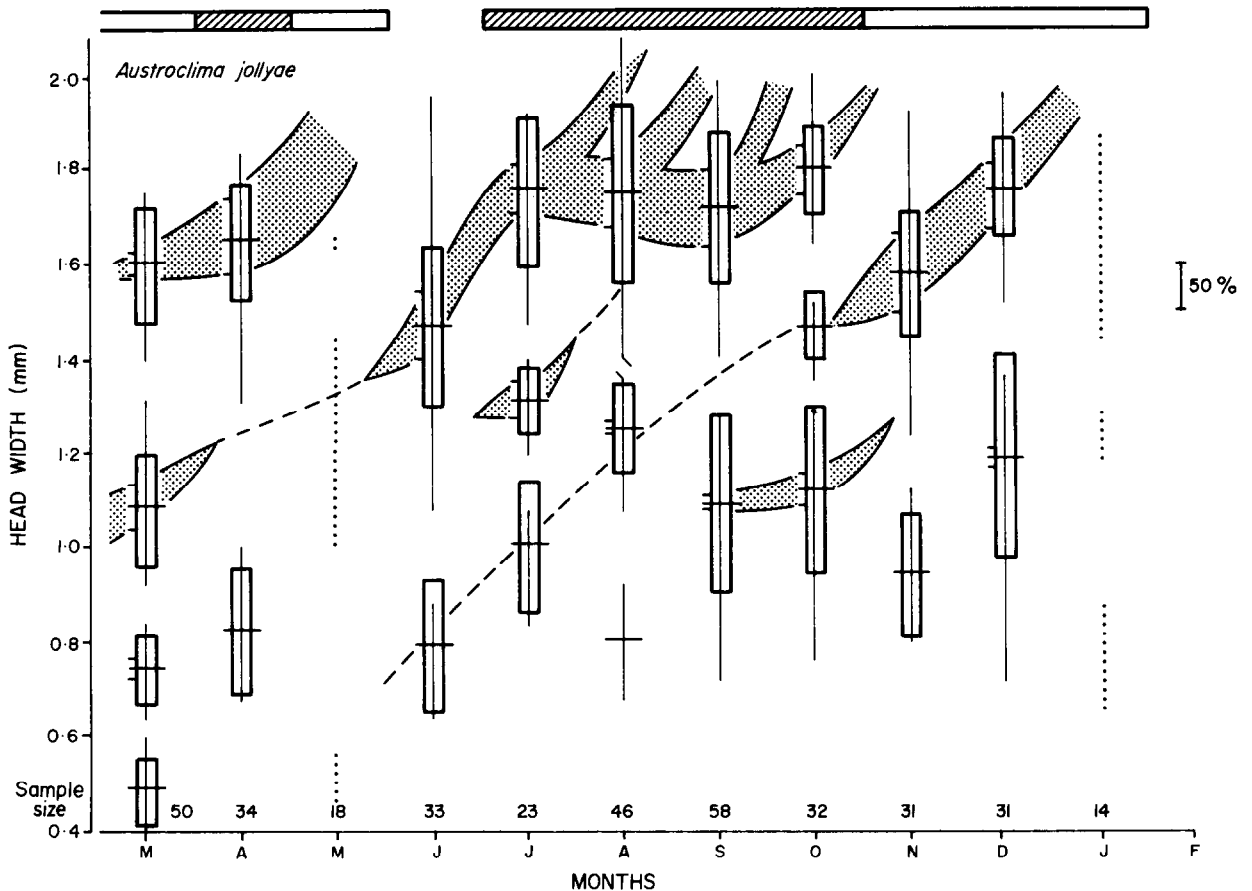


Fig. 2. Seasonal size distributions of *Austroclima jollyae*. Conventions as in Fig. 1.

Deleatidium sp. C

Analysis of the population structure of this species produced so many cohorts that their relationship is unclear. I have interpreted the pattern as being basically bivoltine and consisting of a winter generation (stippled, Fig. 6) which hatches in late autumn, matures in about 6 months and completes emergence to the adult by early summer. This overlaps a spring-summer generation (shaded in Fig. 6). Because some later cohorts consist of more individuals than earlier ones to which they seem connected, there is almost certainly fusion of different cohorts. In addition, the species became more abundant in winter (July–September) during the main emergence period, so that seasonal abundance does not reflect the nymphal life history pattern. Instead, the large winter population of *Deleatidium* sp. C at both riffle sites probably represented

a mobile population most of which hatched elsewhere. This contrasts with the summer population which, through the presence of very small individuals, shows evidence of local hatching.

Deleatidium myzobranchia

Like *Austroclima jollyae*, this species appears to spend only the latter part of its nymphal life in the cascade (Fig. 7), but unlike *A. jollyae*, there was still a clear indication of its growth pattern, *Deleatidium myzobranchia* apparently has a well synchronised univoltine life history and the shortest emergence period of any of the species studied (Fig. 7).

Deleatidium sp. A

This species was abundant in the Cascade Stream in riffle and cascade biotopes (Fig. 3). For life histo-

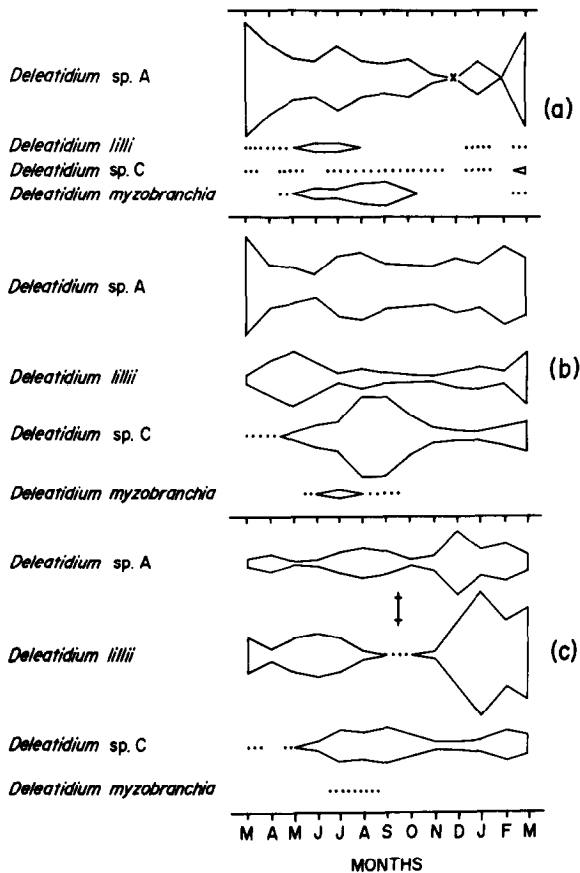


Fig. 3. Seasonal abundance of four *Deleatidium* species in a Cascade Stream cascade (a) and riffle (b) and a Waitakere River riffle (c). Scale, 50 individuals; broken line <10. Total numbers per site: (a), $n = 1\ 505$; (b), $n = 2\ 850$; (c), $n = 2\ 159$.

ry analysis I have used data only from riffle populations to avoid the bias towards larger individuals in the cascade (see below).

The nymphal growth pattern of *Deleatidium* sp. A is extremely unclear. There appear to be two generations: a late winter–spring hatching group (July–October) which overlaps a late spring–summer hatching group. The earlier generation apparently either grows rapidly over summer to emerge during autumn (February–March) or grows more slowly to emerge during winter and spring. Nymphal life of this generation could therefore range from 5 to 9 months (or longer). The later hatching generation apparently grows more slowly to emerge after about 12 months (Fig. 8). These overlapping generations produce an extremely poorly synchronised life history and a year-round potential emer-

gence period (Fig. 8). The life history of this species appears to be further complicated by sex and size related habitat selection during nymphal growth. These produced interesting differences in population size distribution and sex ratios when riffle and adjacent cascade populations were compared. From nine monthly samples obtained on the cascade, eight showed consistent bias towards larger individuals when compared with riffle samples on the same date. This is demonstrated in Fig. 9 in which size distribution of the cascade population is compared with that of riffles immediately upstream and downstream on the same day. Comparison of size of mature nymphs (wing pads >1.6 mm) from riffle and cascade populations using G Tests for similarity between frequencies (Sokal & Rohlf 1969) indicated that size distribution was skewed towards larger females than males in each biotope ($p < 0.005$) and that both sexes of mature nymphs from the riffle tended to be smaller than those from the cascade (Fig. 10). In addition, the cascade population consisted of almost twice as many females than males (χ^2 Test, $p < 0.005$) whereas the riffle population only 10 m downstream did not differ significantly from unity ($p > 0.05$). Combination of these size distribution and sex ratio results suggests a higher survival of females of *Deleatidium* sp. A (which are larger than males) in rapid flow areas. This difference could be related to a physiological ability for larger individuals to retain their position in areas of rapid flow, or, as seems more likely behavioural interactions in which larger individuals (i.e. females) dominate. No other species of *Deleatidium* produced sex ratios which differed significantly from unity.

Discussion

There are few documented studies of life histories of identified species of New Zealand Leptophlebiidae, despite their abundance in stream benthic communities. Most work has involved species of *Deleatidium*, which often dominate the benthos (e.g. Winterbourn 1978, Towns 1979, 1981a), but present particular identification difficulties. Hopkins (1976) identified *D. lillii* as the predominant species of *Deleatidium* in two southern North Island streams, and assumed a bivoltine life history because of two major influxes of early instars, one

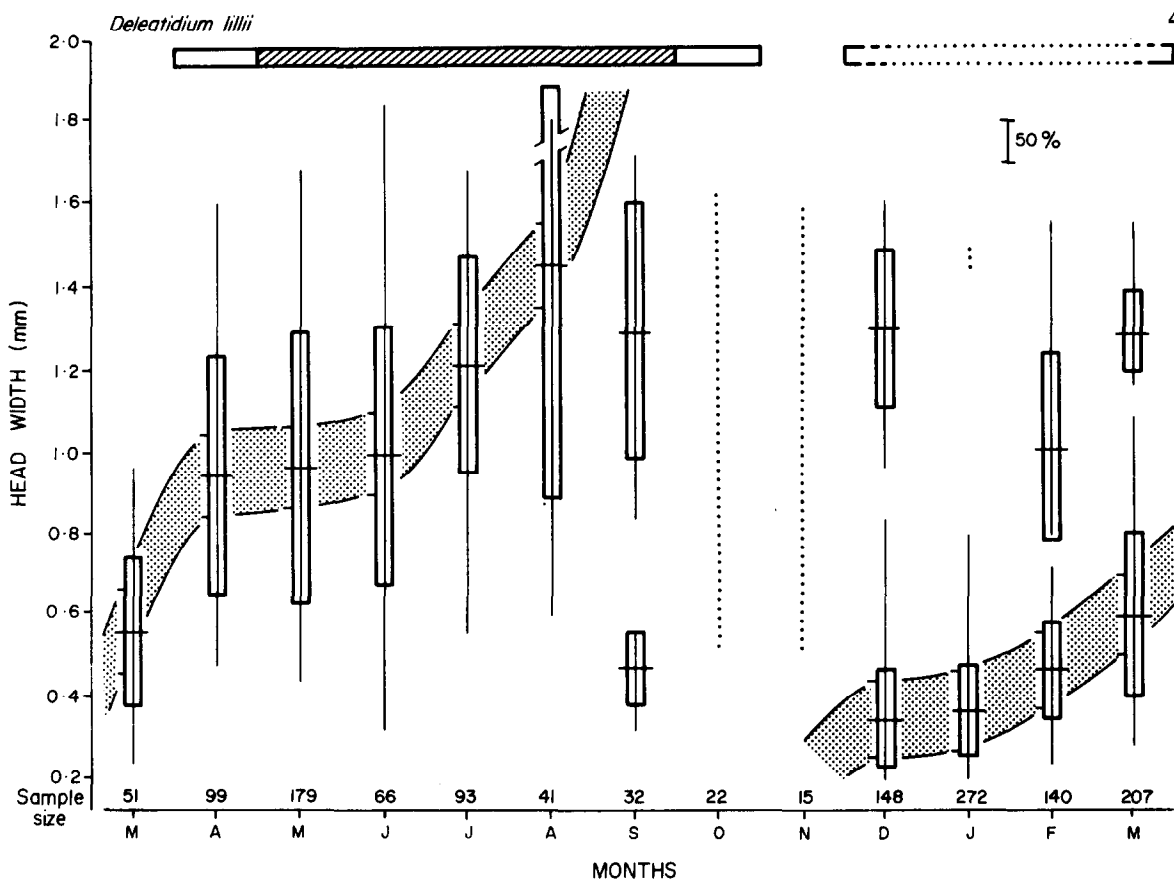


Fig. 4. Seasonal size distribution of *Deleatidium lillii*. Conventions as in Fig. 1.

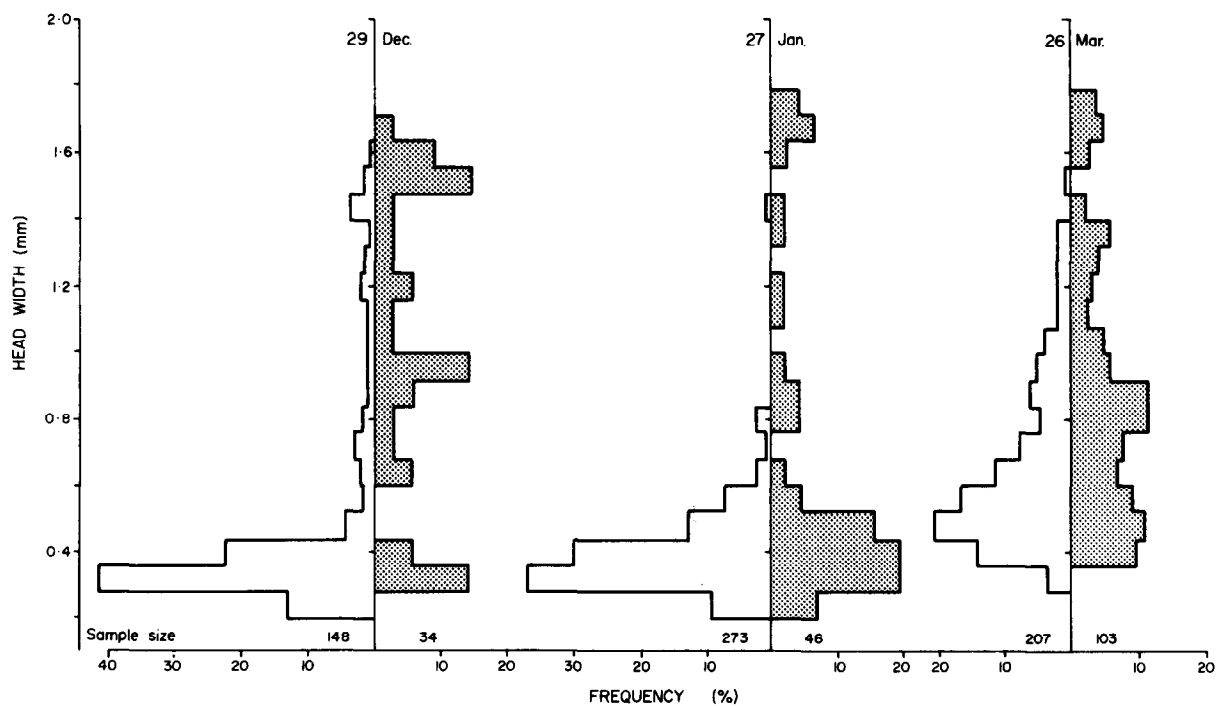


Fig. 5. Size distribution of *Deleatidium lillii* from Cascade Stream (shaded) and Waitakere River (unshaded).

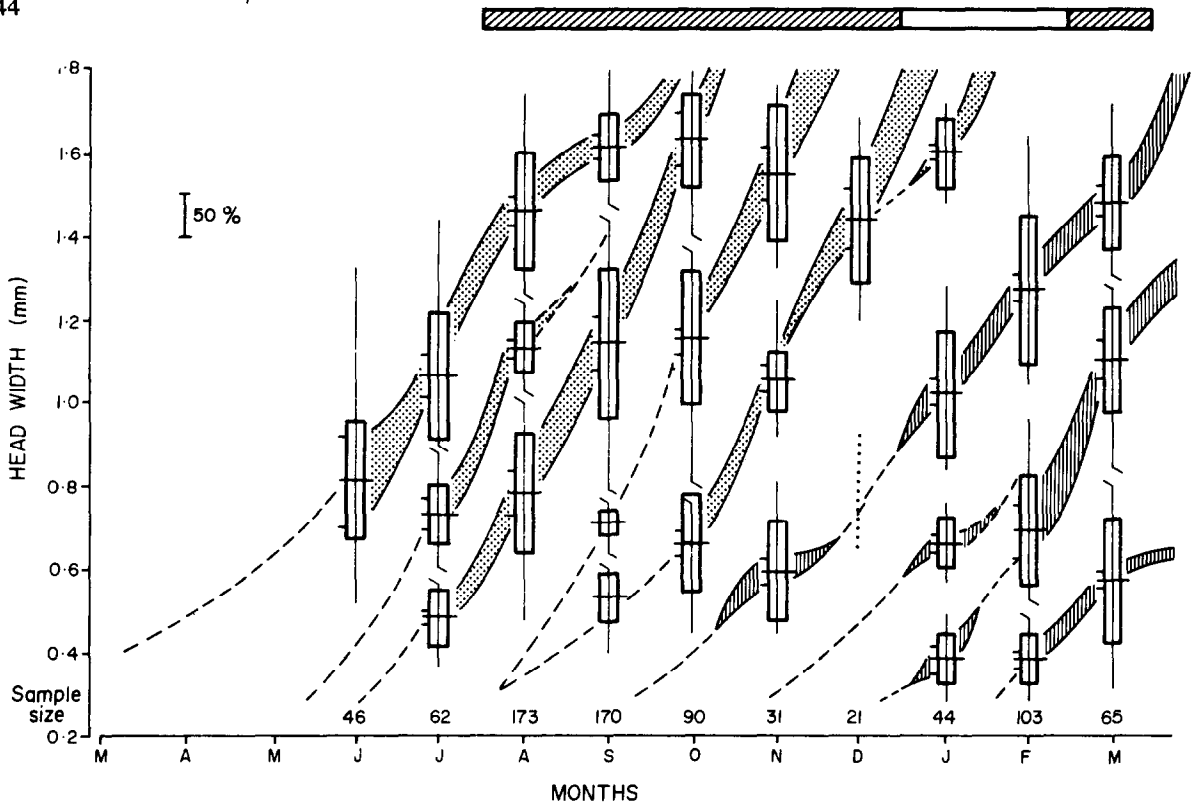
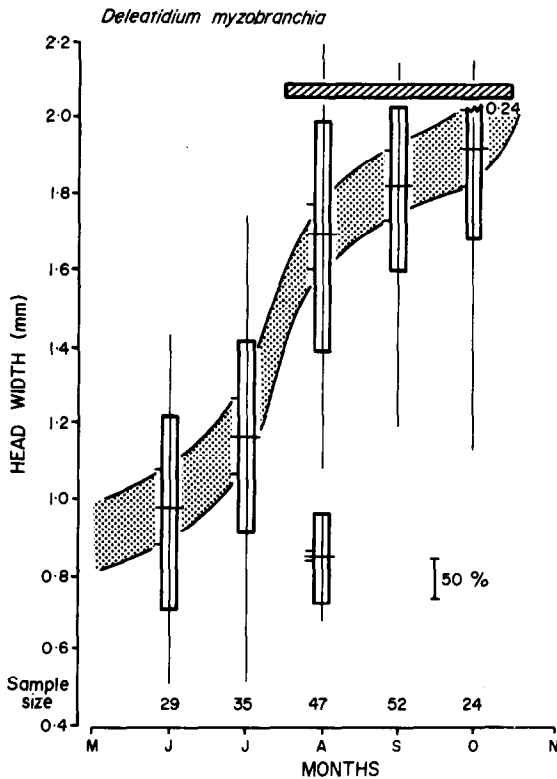


Fig. 6. Seasonal size distribution of *Deleatidium* sp. C. Conventions as in Fig. 1.



in summer and the other in late autumn. In Waitakere River *D. lillii* was clearly univoltine. This apparent difference cannot be reconciled through differences in stream water temperature (and hence nymphal growth rate), since all streams studied had similar temperature regimes (see Allen 1951; Hopkins 1971; Towns 1979). The size frequency data provided by Hopkins (1976) for *Deleatidium* closely resemble those reported in my previous study of unidentified *Deleatidium* spp. (dominated by *D. lillii*), in which a summer and autumn influx of early instars could be identified (Towns 1981a). The present analysis indicates that these size frequency and seasonal abundance differences were composed of more than one species. In Waitakere River *D. lillii* dominated spring-summer samples at its main hatching period, but declined in abundance during late autumn and winter, when there was a marked increase in the abundance of *Deleatidium* sp. C. If, as seems likely, both species occurred in the streams studied by Hopkins (they both occur in

Fig. 7. Seasonal size distribution of *Deleatidium myzobranchia*. Conventions as in Fig. 1.

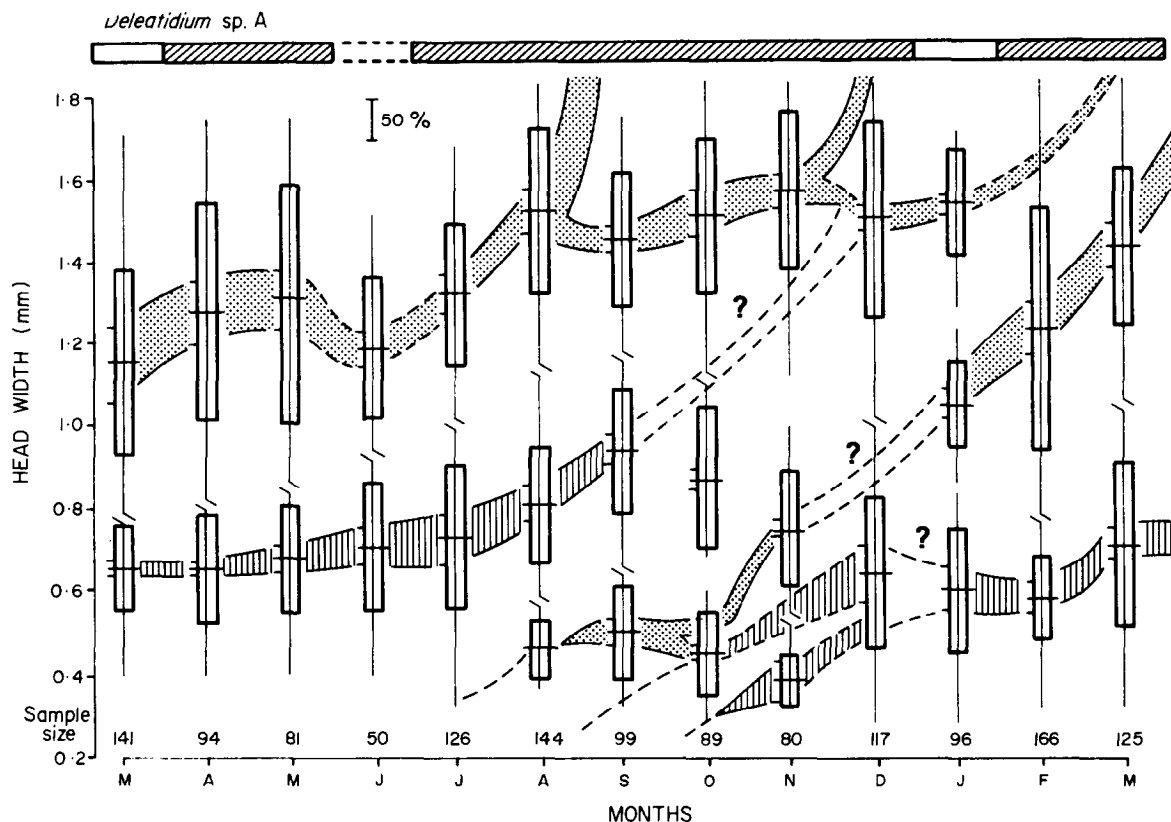


Fig. 8. Seasonal size distribution of *Deleatidium* sp. A. Conventions as in Fig. 1.

streams in the vicinity of his study areas, Towns unpublished data), a similar change in species composition may have occurred.

Winterbourn (1974, 1978) studied life histories of two South Island populations of *Deleatidium* which he assigned to the 'lillii' species group (Winterbourn 1978), but specimens examined by me from his study sites were not *D. lillii* sensu stricto. Life histories of these populations of *Deleatidium* were poorly synchronised, even though the streams were cooler than Waitakere River.

Of the six leptophlebiid species studied in Waitakere River only two, *Deleatidium lillii* and *D. myzobranchia*, had well synchronised, clearly defined growth periods. Even so, the emergence period for *D. lillii* covered at least five months. Therefore, despite soundly based species identification, there is no evidence to support my suggestion that unclear life history patterns found previously in New Zealand Leptophlebiidae were an artifact of overlapping and seasonally staggered growth periods. In-

stead, an array of weakly seasonal and non-seasonal life histories occurred, even in spatially overlapping congeners. This contrasts with most northern hemisphere studies of mayfly life histories which have shown that sympatric congeneric species have similar life history patterns (commonly univoltine), generally with clearly separated growth and emergence periods (e.g. Landa 1968; Grant & Mackay 1969; Flowers & Hilsenhoff 1978; Vannote & Sweeney 1980; Wise 1980). Similar patterns occur in Plecoptera (e.g. Harper 1973) and Trichoptera (e.g. Anderson & Wold 1972). In almost all such studies it has been suggested or implied that seasonally staggered development periods have evolved through interspecific competition and serve to provide most efficient use of resources, ultimately leading to increased niche formation and speciation. This contention is one of the concepts which forms the basis for models of stream ecosystem function (Vannote & Sweeney 1980, Vannote *et al.* 1980).

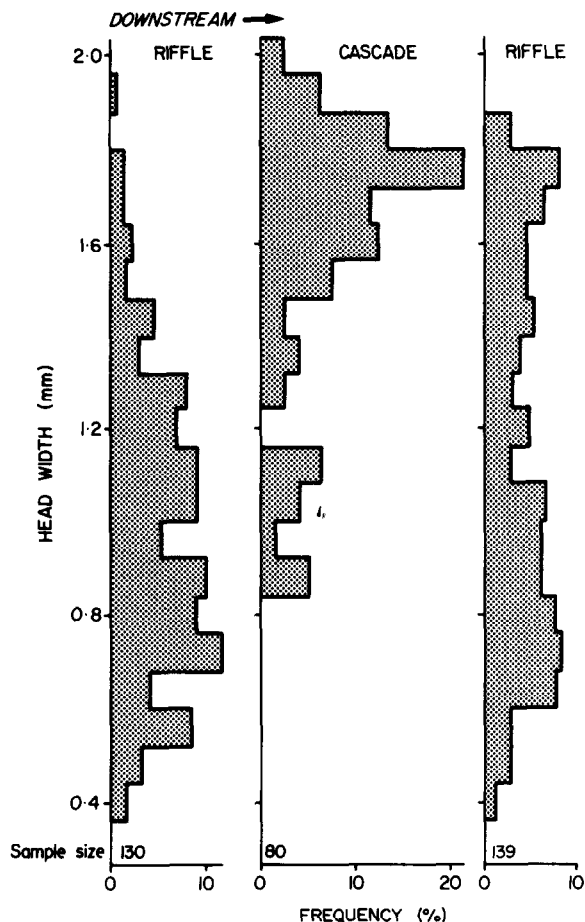


Fig. 9. Size distribution of *Deleatidium* sp. A nymphs in riffle and cascade habitats (25 Aug. 1975).

It has been implied also that functionally (although not taxonomically) related species compete for limited resources (e.g. Townsend & Hildrew 1979). The leptophlebiids studied here all feed indiscriminately on fine particle organic matter and algae (Cowie 1980, pers. obs.) and thus form such a functionally related group. Temporal segregation within this group should be most marked for species occupying the same biotope (riffle or cascade). In fact, the three species present on the cascade, *Deleatidium* sp. A, *D. myzobranchia* and *Austroclima jollyae*, showed extensive temporal overlap of growth and emergence periods but different life history patterns (Fig. 11). This also occurred for the four riffle species, *Deleatidium* sp. A, *Deleatidium* sp. C, *D. lillii* and *Neozephlebia scita*. The only two riffle species which did not have extensively over-

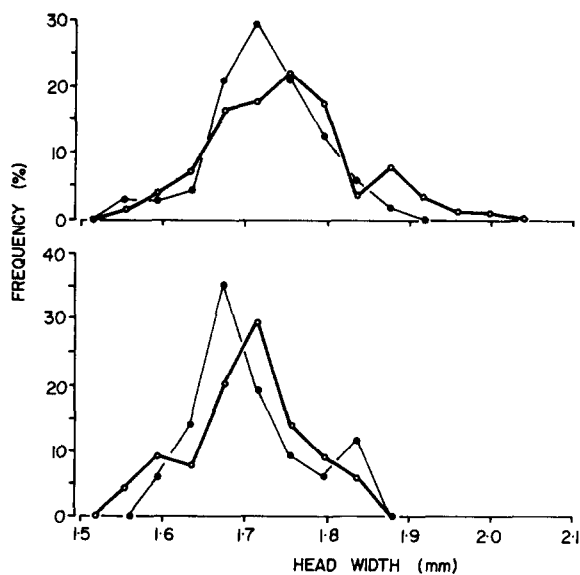


Fig. 10. Size distribution of male (solid symbols) and female (open symbols) nymphs of *Deleatidium* sp. A from a cascade (upper) and a riffle (lower) in Cascade Stream. Sample sizes (n); cascade males, $n = 72$, females, $n = 139$; riffle males, $n = 52$, females, $n = 65$.

lapped emergence periods were *D. lillii* and *N. scita*. However, these are only distantly related taxonomically (see Towns & Peters 1980) and, according to conventional thinking (cf. Lawton & Strong 1981), are less likely to interact effectively than closely related species with similar habitat requirements and morphology, i.e. *Deleatidium*. If such interactions occurred within *Deleatidium*, they were not expressed in life histories of the Waitakere River species, and these data would not even support the possibility that different life history patterns within the genus effectively lead to temporal segregation.

Two possible explanations for the apparently unusual results presented here are: either the role of competition in evolution of stream invertebrate life histories has been incorrectly assessed, or communities in New Zealand streams differ fundamentally from those studied elsewhere.

Terrestrial ecologists have become increasingly aware of the danger of interpreting observed differences in life histories or resource use by closely related species on the assumption that they have evolved as a tactic for ecological differentiation (e.g. Huey 1979; Hairston 1981; Lawton & Strong 1981). However, most observations of stream ecosystems are based on these 'first level' (field) observa-

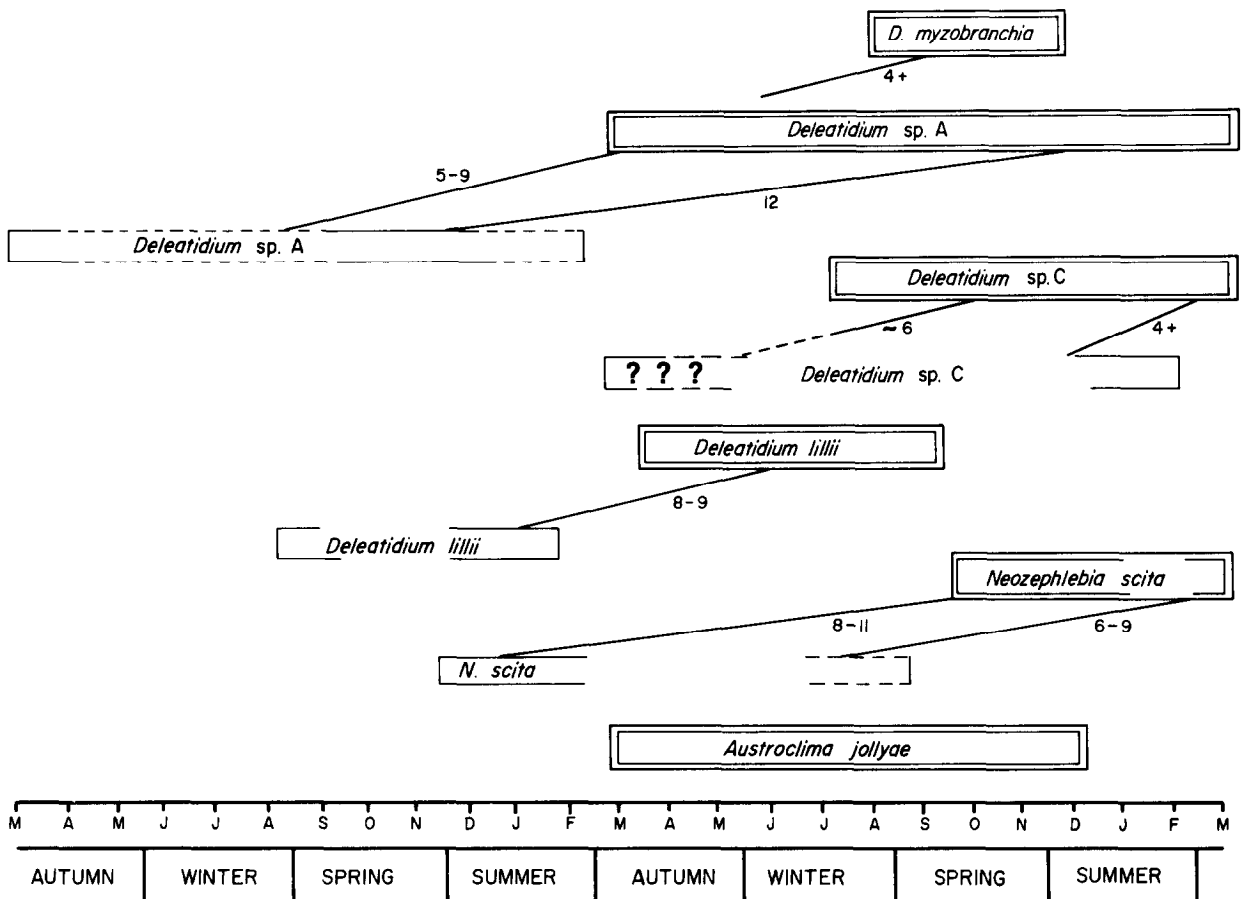


Fig. 11. Summary of life history patterns of Leptophlebiidae in Waitakere River and Cascade Stream, with approximate time (months) to reach maturity. Main hatching (single rectangles) or emergence periods (double rectangles) with solid lines; intermittent hatching or emergence with broken lines.

tions of competition (Huey 1979). Even refinements of this approach, in which there is experimental evidence of differential use of common resources, do not by themselves demonstrate that competition is the driving force determining community structure (Hairston 1981). Indeed, temporal segregation of life histories does not by itself demonstrate differential use of common resources.

Vannote & Sweeney (1980) concede that it is difficult to test whether a species complex represents a high level of community development (an assemblage which has evolved to minimize competition) or is the result of a random gathering of related and regionally available species. They have, however, followed the first approach in their models of evolution of lotic communities, despite the fact that experimental tests of the role of competi-

tion in streams are so few that its actual importance is difficult to assess (Wiley 1981). In fact, several experimental manipulations of benthic density and a study of food availability to seston feeders have failed to demonstrate density related competitive interactions or even partitioning of food resources (Hildebrand 1974; Corkum 1978; Georgian & Wallace 1981). Where density related influences on invertebrate behaviour have been indicated experimentally (e.g. by induction of increased drift), their importance appears to vary according to species and locality (Corkum 1978; Peckarsky & Dodson 1980; Walton 1980), suggesting a far greater complexity of influences on stream community structure than is encompassed by presently available models.

Further weaknesses in the above approach were

indicated in comprehensive literature reviews by Birch (1979) and Lawton & Strong (1981). Birch demonstrated that there are many examples of species in natural populations which share resources and coexist, even where ecological data suggest that one should be excluded. Mechanisms which enable this have particular relevance to streams because of their wide range of microhabitats and inherent environmental instability:

'1. The density of species is kept below that at which they affect each other's chance to survive and reproduce.

2. One species affects the chance of another to survive and reproduce, but the other has a refuge from which it recolonises depopulated places.

3. One species affects the chance of another to survive and reproduce but one is at an advantage at one time and the other at another time or place. The advantages and disadvantages balance out.' (Birch 1979: 217).

Without direct evidence, either through observations of aggression or the effects of manipulating populations or resources, it is usually not possible to exclude alternative explanations where exclusion of one species by another is inferred (Birch 1979).

Consequently, in addition to a lack of experimental evidence supporting assumptions that temporal segregation of life histories has evolved to maximize ecological differentiation, the complexity and range of possible species interactions listed above render the hypothesis excessively simplistic and unlikely to be widely applicable. The previous acceptability of this notion has probably hinged on a relative absence of life history data for congeneric sympatric species which contradict patterns commonly encountered in temperate northern hemisphere streams.

The possibility that New Zealand stream ecosystems are highly distinctive was discussed comprehensively by Winterbourn *et al.* (1981). They concluded that most apparent differences between New Zealand streams and those elsewhere arise because presently available conceptual models of stream ecosystem function are unsound and too narrowly based. One particular characteristic of New Zealand stream ecosystems is the importance of fine particulate organic matter as a food resource which is utilized by a large proportion of the invertebrate community (cf. Winterbourn *et al.* 1981). This

material is probably less limited in supply than the highly seasonal inputs of coarse organic material used as a food base by many stream invertebrates in the northern hemisphere (cf. Anderson & Sedell 1979; Winterbourn *et al.* 1981). Differences in the type and availability of food may prove a useful basis for explaining the high proportion of poorly synchronised life histories in New Zealand stream invertebrates (Towns 1981; Winterbourn *et al.* 1981), but they do not explain extensive temporal overlap of congeneric species. To form a working model, I have followed the suggestion of Lawton & Strong (1981) and present the hypothesis with fewest assumptions. That is, differences in life history patterns within sympatric New Zealand Leptophlebiidae are most likely to have evolved in response to abiotic effects. The present assemblage could therefore be regarded as occurring more or less by chance. Even if there is the potential for competitive interaction these coexisting populations could be maintained by one or more of the mechanisms proposed by Birch (1979).

Summary

Many studies of lotic invertebrate life histories in temperate northern hemisphere have found seasonally staggered hatching, development and emergence periods for sympatric congeneric species. This observation has commonly prompted the suggestion that such seasonality is the result of selective forces which effectively act to minimise interspecific competition.

Life history patterns of six sympatric species of leptophlebiid mayflies in northern New Zealand showed extensive overlap of development and potential emergence periods, in contrast to northern hemisphere patterns. Unlike many mayfly species, which are univoltine, these species showed a mixture of weakly seasonal and poorly synchronised life history patterns. These differences between life histories of New Zealand mayflies and patterns more commonly reported from the northern hemisphere raise the possibility that either New Zealand lotic communities are fundamentally different from those elsewhere, or that the role of interspecific competition requires re-examination.

Current conceptual models of stream ecosystem function emphasise the importance of interspecific

interactions in the evolution of community structure, but experimental tests of competition in streams are so few its actual importance is unclear. Literature reviews of work in terrestrial ecosystems indicate that competition may be too weak or subtle to influence insect community structure. In addition there are several mechanisms which enable species in natural populations to coexist, when ecological data suggest that one should be excluded. Consequently, without rigorously tested support data, it is dangerous to base differences in life histories or resource use by closely related species on the assumption that they have evolved as a tactic for ecological differentiation.

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