# Dietary habits of Australian siphlonurid and oligoneuriid ephemeropteran nymphs

IAN C. CAMPBELL

With 4 figures and 4 tables in the text

## Introduction

Ephemeropteran nymphs form a significant part of the invertebrate fauna of Australian upland streams. An understanding of the ecology of streams depends upon an understanding of the ecological roles of the organisms present. The food of any species is an important factor in its ecological role. The only previously published information on the food of any Australian mayfly is a note by RIEK (1974) that nymphs of *Mirawara* are carnivorous.

In this study, the dietary habits of eleven populations of siphlonurids and oligoneuriids were investigated by an examination of gut contents. A total of ten species were examined, with one species *Coloburiscoides haleuticus*, being investigated at two sites. The species examined and the locations from which the specimens were obtained are tabulated below (Table 1). The locations are indicated in Fig. 1.

## Methods

Methods for investigating the dietary habits of aquatic insects were reviewed by CUMMINS (1973), who recommended an elaborate procedure for the examination of gut contents based on methods developed by BROWN (1960, 1961, 1965). CUMMINS' (1973) suggested technique was not used in the present study since it requires the pooling of the contents of the guts of several animals.

In the present study, two different methods were used. For nymphs of *Coloburiscoides*, *Tasmanophlebia* and *Ameletoides* the method was similar to that employed by FULLER & STEWART (1977,

Table 1. Species examined for gut contents.

| Species | Locality sampled | Site |
|---|---|---|
| *Ameletoides* | | |
|   *A. lacusalbinae* | Lake Albina, New South Wales | 1 |
|   *A.* sp. 1 | Chalet Creek, Victoria | 2 |
| *Mirawara* | | |
|   *M. aapta* | Aberfeldy River, Victoria | 3 |
| *Tasmanophlebia* | | |
|   *T. lacuscoerulei* | Lake Albina, New South Wales | 1 |
|   *T.* sp. 1 | Alpine Creek, New South Wales | 4 |
|   *T.* sp. 2 | Aberfeldy River, Victoria | 3 |
| *Coloburiscoides* | | |
|   *C. haleuticus* | Wellington River, Victoria | 5 |
|   *C. haleuticus* | Goodradigbee River, New South Wales | 6 |
|   *C. giganteus* | Diggers Creek, New South Wales | 7 |
|   *C. munionga* | Eucumbene River, New South Wales | 8 |
|   *C.* sp. 1 | Big Pat's Creek, Victoria | 9 |
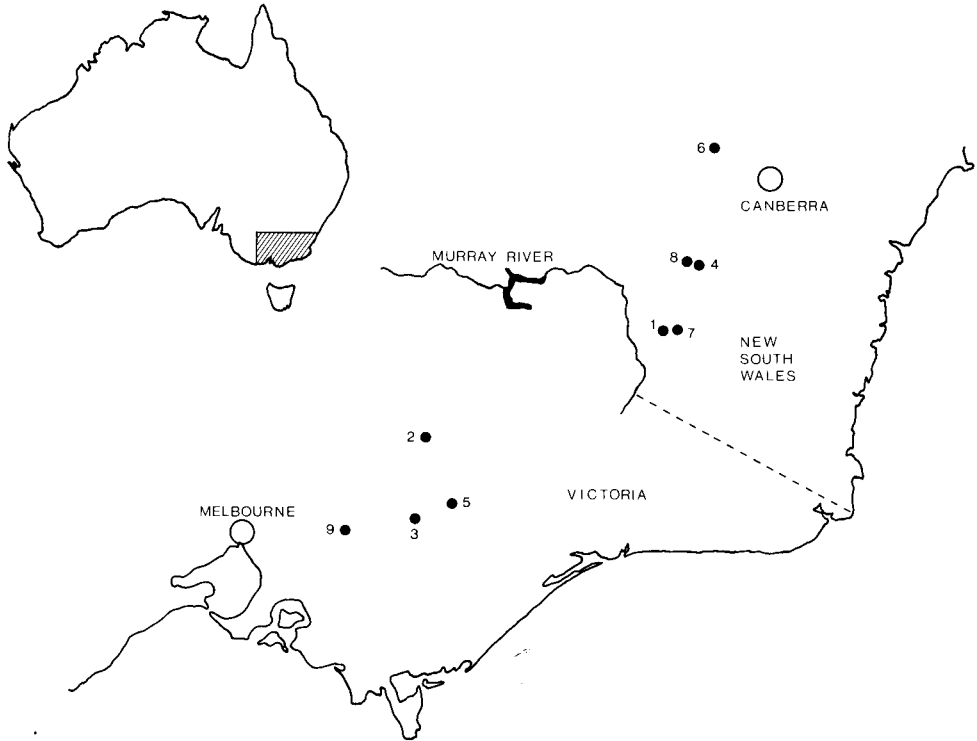
Fig. 1. A map of southeastern Australia indicating the localities from which nymphs used for the dietary studies were obtained. The localities are as follows: 1, Lake Albina; 2, Chalet Creek; 3, Aberfeldy River; 4, Alpine Creek; 5, Wellington River; 6, Goodradigbee River; 7, Digger's Creek; 8, Eucumbene River; 9, Big Pat's Creek.

1979) and more recently by YULE (1982). Each individual nymph was measured and the foregut then dissected out. The gut contents were mounted on a slide in Canada Balsam dissolved in 2-ethoxyethanol. The relative proportions of the different components were determined by measuring their relative areas in four random fields using a Whipple eyepiece micrometer, fitted to a Wild M20 microscope at 40 × magnification.

The gut contents of ten specimens from each population were determined in this fashion. The specimens were selected such that a wide size range of nymphs was investigated. This allowed a check on dietary changes during the life of the nymphs.

A different technique was employed for nymphs of *Mirawara*. *Mirawara* nymphs are predacious and swallow their prey whole. Furthermore, many of the nymphs were found to have only a single prey item in the foregut. For this reason, the gut contents of fifty nymphs were examined, and data on prey items were expressed as the percentage of the nymphs in which they occurred.

## Results

The results for the genera *Ameletoides* and *Tasmanophlebia* are presented in Fig. 2. Data for small nymphs and large nymphs are presented separately on the right hand side of the figure, whilst the average for the species as a whole is presented on the left. Data for *Coloburiscoides* is presented in a similar fashion in Fig. 3, and for *Mirawara* in Fig. 4.
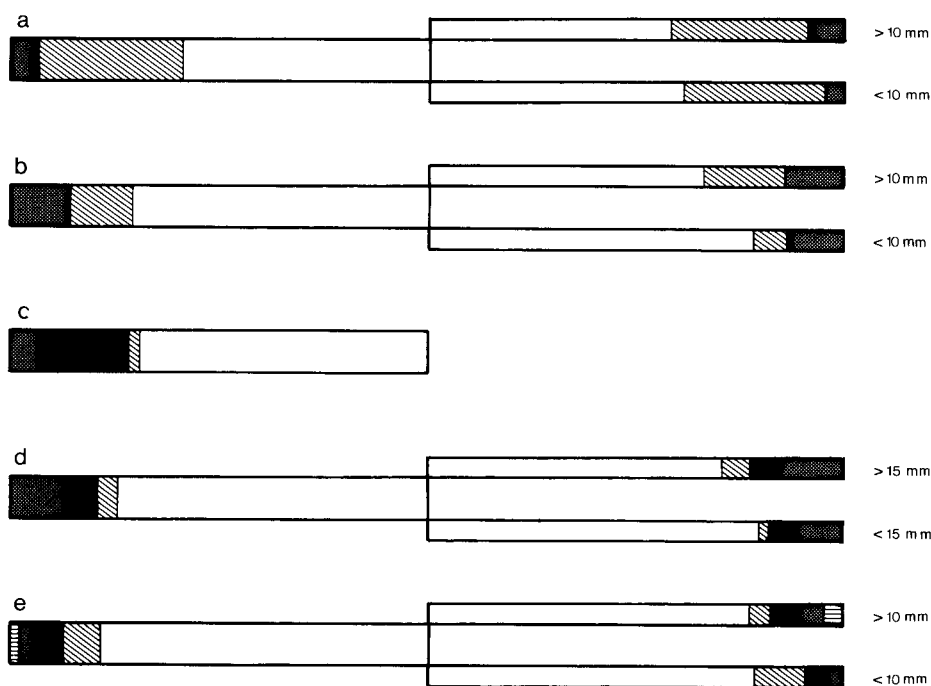
Fig. 2. Percentage composition of gut contents for *Ameletoides lacusalbinae* (a), *Ameletoides* sp. 1 (b), *Tasmanophlebia* sp. 2 (c), *Tasmanophlebia lacuscoerulei* (d), and *Tasmanophlebia* sp. 1 (e). Composition for the total sample is indicated on the left of the figure and for small and large nymphs separately on the right. The size range of the nymphs expressed as total length in mm is indicated on the right. The dietary components indicated are detritus — unshaded, algae — diagonal shading, plant material — solid black, inorganic material — stippled, and wood — horizontal shading.

Four major components of the gut contents of the non-carnivorous mayflies were distinguished in this study. These were detritus, algae, plant material and inorganic material. The detritus component consisted of fine particulate non-cellular organic material of uncertain origin. The algal material included both filamentous and single celled forms, whilst the plant material included coarse particulate cellular material of plant origin excluding wood. Inorganic material consisted of sand and other mineral particles.

Two other minor components of the gut contents were also recognized. Wood fragments were present in the guts of some specimens of *Tasmanophlebia* sp. 1 and comprised nearly 20 % of the gut contents of one specimen. Fragments of insects were found in the gut of one specimen of *Coloburiscoides haleuticus* from the Wellington River. The fragments were mostly fragments of wing.

## Discussion

*Ameletoides* nymphs live within a wide variety of habitats. *A. lacusalbinae* occurs in both lakes and streams. Within streams it is found both in pools and in the fastest riffles of steep stony streams. *Ameletoides* sp. 1 has only been taken in streams; however, it occurs in both pools and riffles. In all cases, the pools had gravel rather than silt substrates.
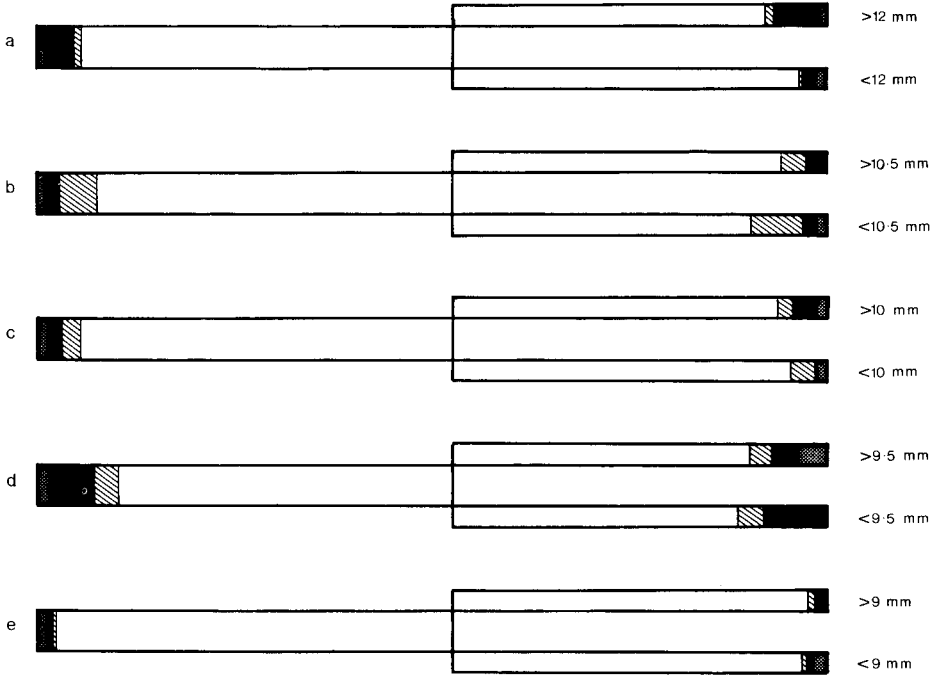
Fig. 3. Percentage composition of gut contents of *Coloburiscoides giganteus* (a), *C. munionga* (b), *C. haleuticus* from the Wellington River (c), *C. haleuticus* from the Goodradigbee River (d), and *C.* sp. 1 (e). Composition for the total sample is indicated on the left of the figure and for the small and large nymphs separately on the right. The size range of the nymphs expressed as total length in mm is indicated to the right. The dietary components indicated are detritus — unshaded, algae — diagonal shading, plant material — solid black, and inorganic material — stippled.
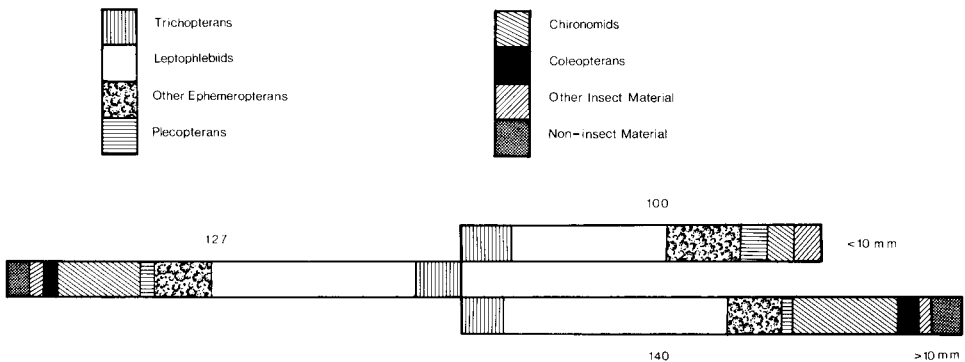


Fig. 4. Gut contents of *Mirawara aapta* nymphs. The results are expressed as the percentage of nymphs examined whose guts contained one of the eight components listed in the figure. Data from nymphs with empty guts were not considered. Because a single nymph sometimes had more than one of the components in its gut, the total percentages may add up to more than 100. The actual total percentage is indicated in the figure. Data for the whole sample are presented on the left and for nymphs larger than and smaller than 10 mm total length separately on the right.

*Ameletoides* nymphs appear from their gut contents to be epilithic feeders. In both species the gut contents consisted mostly of detritus and algae (Fig. 2). Inorganic material was the only other component of any significance present. *Ameletoides* nymphs have a single large mandibular "tooth" which could be utilized as a scraping implement. Significantly, the tooth is of variable size, which is consistent with it being worn down with use during the intermoult period. It is renewed each moult.

There were only slight differences in the relative proportions of the three major components of the gut contents between small (< 10 mm total length) and large (> 10 mm total length) nymphs. However, there did appear to be differences in the type of algae being consumed. In both species, virtually all of the algae present in the guts of the smaller nymphs were diatoms, whereas the larger nymphs also contained large amounts of a brown coloured colonial alga, possibly a species of *Botryococcus*.

Both of the species would be categorized as "algal scrapers" according to the classification proposed by CUMMINS & KLUG (1979). However, detritus is a more abundant material in the gut than algae, and, although some of the detrital material may consist of algal fragments and cell contents, most of the detritus probably consists of bacteria, fungi and non-living organic material also scraped from the rock surfaces. Which of the two materials, algae or detritus, is a more important food source could only be determined by assimilation studies. ROUNICK et al. (1982), for example, have suggested that *Deleatidium* (Leptophlebiidae) nymphs selectively assimilate algae, even though they apparently feed relatively non-selectively on both algae and detritus obtained from the surface of stones.

WINTERBOURN et al. (1981) have recently used the term "browsers", which BARMUTA & LAKE (1982) have suggested encompasses collector-gatherers capable of utilizing the epilithos. This would seem to be preferable to the description "algal scrapers" for organisms consuming both algae and detritus, since it does not contain an implicit assumption of the relative food value of the algae and detritus. Nor does it restrict the category to organisms which obtain the material from the stones by scraping. Many leptophlebiid nymphs are also epilithic feeders, but, from the morphology of their mouthparts, they appear to obtain their food by scrubbing. In spite of this difference, they would seem to belong to the same functional category as *Ameletoides* nymphs.

*Ameletoides* sp. 1 consumed less algae than *A. lacusalbinae* (Fig. 2). The difference was significant at the 0.01 level using the MANN-WHITNEY test (CONOVER 1971). The difference between the two may simply be a reflection of a difference in algal abundance in the habitats of the two species. *Ameletoides lacusalbinae* was collected in Lake Albina, an alpine lake above the tree line. The nymphs occurred on rocks in shallow (< 0.4 m) water around the edge of the lake. *Ameletoides* sp. 1, on the other hand, was collected from Chalet Creek, a small stream flowing in a small steep valley and heavily shaded by forest. As a consequence, the amount of light available to support algal photosynthesis was considerably less at the Chalet Creek site than at the Lake Albina site.

In spite of the differences in algal consumption between the two species, they occupied very similar feeding niches as measured by HORN's (1966) Coefficient of Dietary Overlap. The coefficient is calculated using the equation:

$$C = \frac{2 \sum\limits^{s} X_i Y_i}{\sum\limits^{s} X_i^2 + \sum\limits^{s} Y_i^2}$$

where: C = overlap coefficient,
     s = number of food categories,

$X_i$ = that proportion of the total diet of species X from a given category of food i,
$Y_i$ = that proportion of the total diet of species Y from a given category of food i.

Possible values of C range from 0 (no overlap) to 1 (complete overlap, identical diets), and values greater than 0.60 indicate significant overlap (FULLER & STEWART 1979). The value for the coefficient between *A. lacusalbinae* and *A.* sp. 1 was 0.95.

Comparing the gut contents between small (< 10 mm total length) and large (> 10 mm) nymphs of *Ameletoides* sp. 1 showed some differences (Fig. 2). Smaller nymphs apparently consumed more detritus and less algae. The difference in the amount of algae was significant at the 0.10 level using the MANN-WHITNEY test (CONOVER 1971).

*Tasmanophlebia* nymphs are primarily detritivores. Their guts generally contained less algae and more plant material than *Ameletoides* nymphs (Fig. 2). Three species were investigated: *Tasmanophlebia lacuscoerulei*, *T.* sp. 1 and *T.* sp. 2. However, only six nymphs of *T.* sp. 2 were examined, since this was the largest number of nymphs of this species available from a single location. Combining nymphs from different locations would add a further complication to data interpretation.

*Tasmanophlebia* nymphs are, for the most part, more restricted in their habitats that those of *Ameletoides*. *Tasmanophlebia lacuscoerulei* is the exception, although it is restricted in its distribution, occurring only in the five glacial lakes near the summit of Mt. Kosciusko. Within the lakes it can be collected both on stony substrates as well as on finer materials — silt and sand. The nymphs are rarely abundant around the lake edges, but may be more abundant deeper in the lakes. TIMMS (1980), in a fairly superficial survey of the benthos of four of the Kosciusko lakes, recorded *T. lacuscoerulei* (misidentified as *T. nigrescens*) only from a depth of 4 m in Blue Lake, where he recorded a population density of 11 nymphs $\cdot$ m$^{-2}$.

*Tasmanophlebia* sp. 1 is found at the edges of stream pools. *T.* sp. 1 nymphs are almost always associated with silt and finely divided organic material, but were occasionally observed on sand. If provided with a silty substrate in the laboratory, they quickly buried themselves.

*Tasmanophlebia* sp. 2 occurs in streams over a wider geographical area than any other species from this genus. It is always associated with fine gravel and coarse sand. Attempts to study the life history of this species in the Aberfeldy River were thwarted when no nymphs could be collected during the winter months of either 1978 or 1979. The nymphs were only half grown at the time, so the disappearance could not have been due to emergence. It is possible therefore that there is a habitat change during thy nymphal life, with the nymphs moving down into the substrate or into deep water in mid-stream.

All of the *T.* sp. 2 nymphs studied were of similar size, with a range of total length from 10.5 to 12.5 mm. As a consequence, no analysis of variation in diet with size was attempted for this species.

The results for *Tasmanophlebia lacuscoerulei* from Lake Albina show more algae being consumed by larger (> 15 mm total length) than by smaller (< 15 mm) nymphs. However, the differences were not significant when tested by the MANN-WHITNEY test. *Tasmanophlebia* sp. 1 did show a significant difference between large (> 10 mm total length) and small (< 10 mm) nymphs. Smaller nymphs consumed more algae, and the difference was significant at the 0.10 level using the MANN-WHITNEY test. This was the only significant difference between the size classes.

Although it might have been expected that *T. lacuscoerulei* would consume more algae, living as it does in shallow water of unshaded Lake Albina, than does *T.* sp. 1, which lives in a heavily shaded stream, this was not the case. In fact, gut analyses showed that *T. lacuscoerulei* consumed less algae, and the difference was significant at the 0.05 level.

In Lake Albina, *T. lacuscoerulei* co-exist with *Ameletoides lacusalbinae* which, as previously discussed, is an algal scraper. Although there seemed to be no preferred microhabitat for *T. lacuscoerulei* in Lake Albina, it presumably is feeding on detritus collecting in rock crevices. It would be interesting to compare the results from the Lake Albina population with gut contents of the population in nearby Blue Lake, from which *Ameletoides* is absent, to see whether more algae is consumed by that population.

*Tasmanophlebia* sp. 2, in the Aberfeldy River, consumed the least proportion of algae and the largest proportion of plant matter of any of the *Tasmanophlebia* species examined. The high proportion of plant material is not surprising in view of the habitat of the species, but the low proportion of algae is unexpected.

HORN's (1966) coefficient indicates a high degree of dietary overlap between all of the *Tasmanophlebia* species. The coefficient for *T.* sp. 1 and *T. lacuscoerulei* had a value of 0.99, that between *T.* sp. 1 and *T.* sp. 2 was 0.97 and that between *T.* sp. 2 and *T. lacuscoerulei* was 0.98.

The degree of dietary overlap between the species of *Tasmanophlebia* and *Ameletoides* investigated was high in every case (Table 2). The overlap was lower for *A. lacusalbinae* because of the relatively higher proportion of algae in the diet of that species. The only co-existing species of the set are *A. lacusalbinae* and *T. lacuscoerulei*, and, although the degree of overlap between that pair was lower than for all but one other pair, it was still so high as to preclude dietary differences as more than a minor factor in niche separation between the two species.

*Coloburiscoides* nymphs require flowing water to survive. In the laboratory they die in a few days if kept in still or turbulent water. They are widespread in the rapidly flowing erosional sections of streams on the Australian mainland south of about 35° and east of 145°. The nymphs of all of the species other than *Coloburiscoides* sp. 1 are to be found under rocks of cobble size or larger in parts of the stream where the current is rapid. Their heavily sclerotized and spiny gills are presumably used to anchor them in position between the rock and the substrate beneath it. *Coloburiscoides* sp. 1 is always associated with wood, often in streams where rocks are scarce. I have found it abundant in *Melaleuca* sp. and *Leptospermum* sp. roots growing into streams, and it is also common on logs so long as crevices are present in which it can shelter.

All of the populations of *Coloburiscoides* investigated were predominantly detritivores (Fig. 3). WISELY (1961) has investigated the feeding of *Coloburiscus* nymphs and demonstrated that they are filter feeders. Since the mouthparts and forelegs of *Coloburiscus*

Table 2. Values of HORN's (1966) coefficient of dietary overlap calculated between species of *Ameletoides* and *Tasmanophlebia*.

|  | *Tasmanophlebia* | | |
|  | *lacuscoerulei* | sp. 1 | sp. 2 |
| --- | --- | --- | --- |
| *Ameletoides lacusalbinae* | 0.85 | 0.89 | 0.91 |
| *A.* sp. 1 | 0.94 | 0.99 | 0.98 |

and *Coloburiscoides* are extremely similar morphologically, it is likely that *Coloburiscoides* is also a filter feeder. This proposition is reinforced by the fact that *Coloburiscoides* nymphs only survive in the laboratory in flowing water.

The foregut contents of *Coloburiscoides* nymphs were invariably found to consist of balls of detrital material, which is also consistent with the method of feeding described by WISELY (1961) for *Coloburiscus*: he noted "sometimes a peculiar movement takes place; the head is withdrawn posteriorly against the prothorax and then pushed anteriorly again, the complete cycle lasting about a second ... Possibly this movement is a swallowing and compressing movement which may aid food passing posteriorly through the alimentary canal."

Filter feeding is not uncommon in the Ephemeroptera. WALLACE & MERRITT (1980) noted that it has long been known in *Isonychia*, another oligoneuriid genus (CLEMENS 1917), and is now also known or likely in at least some species of baetids, leptophlebiids and ephemerellids.

There is little indication from the gut contents that *Coloburiscoides* nymphs were discriminatory in their dietary habits. The Eucumbene River is completely unshaded, and algae were probably more abundant there than at the other localities. Big Pat's Creek, on the other hand, was the most heavily shaded, and nymphs from that locality (*Coloburiscoides* sp. 1) had the least algae in the foregut.

The amount of plant material was surprisingly high in the guts of nymphs of *Coloburiscoides haleuticus* at the Goodradigbee River site. There was a significant difference at the .05 level, using the MANN-WHITNEY test, between the proportion of plant material in the guts of the population at Goodradigbee and the proportion in the population of ·the same species at Wellington River. Large amounts of *Casuarina cladodes* were usually present in the Goodradigbee, and their breakdown may have given rise to high levels coarse particulate plant material in the water column.

Only one species of *Coloburiscoides*, *C. munionga* showed differences between large and small nymphs which were significant when tested with the MANN-WHITNEY test. For this species, smaller nymphs consumed more algae than the larger nymphs. The difference was significant at the 0.10 level. *Coloburiscoides haleuticus* nymphs in the Wellington River consumed more plant material when they were larger. Plant material was only recorded in a single sample from the smaller nymphs, so that a confidence level could not be placed on the significance; but plant material was recorded in six of the twenty samples from larger nymphs, so the difference may well be important.

The degree of dietary overlap, as determined by HORN's (1966) coefficient, was extremely high between all the species of *Coloburiscoides* (Table 3). It indicates that composition of the diet as it was categorized in this study, was virtually identical between the

Table 3. Values for C, the coefficient of dietary overlap (HORN 1966) between species and population of *Coloburiscoides* (figures rounded to two decimal places).

|  | C. giganteus | C. munionga | C. haleuticus (Goodradigbee R.) | C. haleuticus (Wellington R.) |
|---|---|---|---|---|
| C. munionga | 0.99 | – |  |  |
| C. haleuticus (Goodradigbee R.) | 0.99 | 0.99 | – |  |
| C. haleuticus (Wellington R.) | 1.00 | 1.00 | 0.99 | – |
| C. sp. | 1.00 | 0.99 | 0.98 | 1.00 |

Table 4. Values for C, the coefficient of dietary overlap (HORN 1966) between species and popula-
tions of *Coloburiscoides* and species of *Ameletoides* and *Tasmanophlebia*.

|                  | C. giganteus | C. munionga | C. haleuticus | C. haleuticus | C. sp. 1 |
| ---------------- | ------------ | ----------- | ------------- | ------------- | -------- |
| A. lacusalbinae  | 0.84         | 0.89        | 0.86          | 0.89          | 0.83     |
| A. sp. 1         | 0.95         | 0.97        | 0.96          | 0.97          | 0.94     |
| T. sp. 2         | 0.95         | 0.95        | 0.94          | 0.98          | 0.92     |
| T. lacuscoerulei | 0.99         | 0.99        | 0.99          | 1.00          | 0.97     |

species. Any niche differentiation between them is presumably based, therefore, on some
other factors.

Comparing dietary habits of the species of *Coloburiscoides* with those of *Ameletoides*
and *Tasmanophlebia* also indicates strong dietary overlap (Table 4). Overlap was least for
all *Coloburiscoides* species and *Ameletoides lacusalbinae*, due to the higher proportion of
algae in the diet of *A. lacusalbinae*. But even for this species the overlap was well above
the level considered significant (FULLER & STEWART 1979). Since the three genera exploit
different habitats within the stream, there would be no reason for them to have de-
veloped niche differentiation through dietary differences, so long as the same foods were
available to a similar degree in each of the habitats.

*Mirawara* nymphs have only been collected in streams where loose stones are present.
They are most numerous in the Aberfeldy River at sites where there are considerable ac-
cumulations of cobbles. These presumably provide sheltering places for the nymphs dur-
ing the day, as wells being sites where prey species are abundant. Current speed does not
seem a major factor, although they are rarely present at water velocities greater than
$1 \, m \cdot s^{-1}$. In the sites I have collected *Mirawara*, nymphs have been most abundant in
stony pools, but quite common in riffles with current speeds up to about $0.5 \, m \cdot s^{-1}$.

*Mirawara aapta* nymphs are carnivorous, and therefore the species has no dietary
overlap with any of the preceding species. As noted above, these nymphs swallow their
prey whole and, in the case of nymphs which had recently fed, this made identification of
prey species fairly simple. Several case-dwelling trichopterans still inside their cases were
retrieved from the foreguts of large *Mirawara* nymphs!

Leptophlebiid mayfly nymphs were the most common prey item found in the guts of
*Mirawara* nymphs. Many of the nymphs were whole and could be positively identified as
*Atalophlebioides* sp. In some cases, only leptophlebiid fragments were found and, since no
species of leptophlebiid other than *Atalophlebioides* sp. was positively identified from the
guts, it is presumed that these fragments were also *Atalophlebioides*. These are indicated in
Fig. 4 as leptophlebiids.

At least eight prey species were found in the guts of the fifty *Mirawara* nymphs ex-
amined. These included two other species of mayfly (*Tasmanocoenis* sp. and *Centroptilum*
sp.), one species of plecopteran (*Dinotoperla* sp.) and two species of trichopterans.

CUMMINS & KLUG (1979) have suggested that food is generally limiting for predatory
stream invertebrates, and HYNES (1970) suggests that predatory insects in streams tend to
be prey-selective. This is certainly true of several species of carnivorous plecopterans
(HYNES 1976). It is not possible, on the basis of the data available from this study, to reach
a conclusion as to the degree of prey selection shown by *Mirawara* nymphs. *Atalophle-
bioides* nymphs were extremely abundant on the tops of rocks in the Aberfeldy River,
and their abundance in the diet of *Mirawara* may simply be a reflection of this.

The dietary habits of the small (< 10 mm total length) and large (> 10 mm total length) nymphs appear to be similar (Fig. 4). However, the large nymphs appear to consume chironomids more frequently and trichopterans less frequently than the smaller nymphs.

## References

BARMUTA, L. A. & LAKE, P. S., 1982: On the value of the river continuum concept. — *N. Z. J. Mar. Freshwat. Res.* **16**: 227—229.

BROWN, D. S., 1960: The ingestion and digestion of *Cloëon dipterum* L. — *Hydrobiologia* **16**: 81—96.

— 1961: The food of the larvae of *Cloëon dipterum* L. and *Baetis rhodani* (PICTET). — *J. Anim. Ecol.* **30**: 55—75.

— 1965: The morphology and function of the mouthparts of *Cloëon dipterum* L. and *Baetis rhodani* (PICTET). — *Proc. Zool. Soc. Lond.* **136**: 147—176.

CLEMENS, W. A., 1917: An ecological study of the mayfly *Chirotenetes.* — *Univ. Toronto Biol. Ser.* **17**: 1—43.

CONOVER, W. J., 1971: *Practical Nonparametric Statistics.* — Wiley International, New York.

CUMMINS, K. W., 1973: Trophic relations of aquatic insects. — *Ann. Rev. Entomol.* **18**: 183—206.

CUMMINS, K. W. & KLUG, M. J., 1979: Feeding ecology of stream invertebrates. — *Ann. Rev. Ecol. Syst.* **10**: 147—172.

FULLER, R. L. & STEWART, K. W., 1977: The food and habits of stoneflies (Plecoptera) in the Upper Gunnison River, Colorado. — *Environ. Entomol.* **6**: 293—302.

HORN, H. S., 1966: Measurement of "overlap" in comparative ecological studies. — *Amer. Nat.* **100**: 419—424.

HYNES, H. B. N., 1970: *The Ecology of Running Waters.* — Liverpool Univ. Press, Liverpool.

— 1976: Biology of Plecoptera. — *Ann. Rev. Ent.* **21**: 135—153.

RIEK, E. F., 1974: Ephemeroptera. — In: MACKERRAS, I. M. (ed.), *The Insects of Australia.* CSIRO and Melbourne Univ. Press, Melbourne.

ROUNICK, J. S., WINTERBOURN, M. J. & LYON, G. L., 1982: Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. — *Oikos* **39**: 191—198.

TIMMS, B. V., 1980: The benthos of the Kosciusko glacial lakes. — *Proc. Linn. Soc. N. S. W.* **104**: 119—125.

WALLACE, J. B. & MERRITT, R. W., 1980: Filter-feeding ecology of aquatic insects. — *Ann. Rev. Entomol.* **25**: 103—132.

WINTERBOURN, M. J., ROUNICK, J. S. & COWIE, B., 1981: Are New Zealand stream ecosystems really different? — *N. Z. J. Mar. Freshwat. Res.* **15**: 321—328.

WISELY, B., 1961: Studies on Ephemeroptera I — *Coloburiscus humeralis* (WALKER); early life history and nymph. — *Trans. Roy. Soc. N. Z. Zool.* **1**: 249—257.

YULE, C. M., 1982: Studies on the biology of *Dinotoperla* species (Plecoptera: Gripopterygidae) in Victoria. — Unpubl. M. Sc. thesis, Zoology Dept., Monash Univ.

Author's address:

Water Studies Centre, Chisholm Institute of Technology, P. O. Box 197, Caulfield East, Victoria 3145, Australia