

## Diel changes in the abundance and size composition of invertebrate drift in five rivers in South Island, New Zealand

P. M. SAGAR

G. J. GLOVA

Freshwater Fisheries Centre  
Ministry of Agriculture and Fisheries  
P. O. Box 8324, Riccarton  
Christchurch, New Zealand

**Abstract** Drift was collected over 24-h periods in five rivers in South Island, New Zealand, to determine whether diel periodicity was consistent across a range of river types, and whether the pattern was similar for different life stages/sizes of selected taxa. Total drift density (numbers per 100 m<sup>3</sup>) of aquatic invertebrates was greater at night than during the day in all rivers; peak abundance occurred shortly after sunset in clear water rivers and shortly before sunrise in a turbid, glacier-fed river. Densities of drifting *Deleatidium* spp., *Nesameletus* spp. (both Ephemeroptera), *Aoteapsyche* spp., and Hydrobiosidae (both Trichoptera), were generally greater at night than during the day. However, the timing of peak abundance in the drift for other common taxa varied between rivers. Larger *Deleatidium* spp. larvae (> 1.00 mm head width) were more common in the drift at night than during the day in all rivers. However, this was not apparent for *Aoteapsyche* spp. and Hydrobiosidae, for which diel differences in the size of drifting animals were not consistent even within the same river. The propensity for some aquatic invertebrates to drift at night may influence fish feeding behaviour, particularly with respect to the timing of feeding and the species or life history stages of their prey.

**Keywords** aquatic invertebrates; diel periodicity; *Deleatidium* spp.; drift density; life stages; drift-feeding fish

## INTRODUCTION

Drift is the downstream transport of organisms in running waters. The phenomenon and its causes have been studied extensively outside New Zealand (for reviews see Waters 1972; Müller 1974; Statzner et al. 1984; Brittain & Eikland 1988), and it has been established that the abundance of drifting invertebrates is generally greater at night than during the day. Not all taxa or life stages of invertebrates occur in the drift and this has led to much speculation as to whether entry into the drift is active or passive, and whether drifting enhances the survival of aquatic invertebrate larvae.

Drifting invertebrates are an important source of food for some species of fish in New Zealand streams. Some of these fish feed selectively on larger prey, examples being the common river galaxias, *Galaxias vulgaris* Stokell (Cadwallader 1975; Glova & Sagar 1989); juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum) (Sagar & Glova 1987, 1988); and juveniles of rainbow trout, *Oncorhynchus mykiss* (Richardson), and of brown trout, *Salmo trutta* Linnaeus (Glova & Sagar 1991).

Despite the importance of drift to fish and the interest in the mechanisms of drift in other countries, relatively few studies have examined the phenomenon in detail in New Zealand rivers. McLay (1968), Burnet (1969), Watson (1971), Cadwallader (1975), Collier & Wakelin (in press), and Sagar & Glova (in press) have confirmed for New Zealand that, in general, drift density is greater at night than during the day, and that some taxa are usually night-active, day-active, or show no diel pattern of activity. Other aspects of the drift phenomenon studied in New Zealand include measurements of the distance drifted (McLay 1970); the effects of artificially induced fluctuations in flow on the numbers of invertebrates drifting (Irvine & Henriques 1984); the effect of a cave on the composition and density of drift in a stream (Death 1989); the effect of floods on drift in three West Coast streams (Graesser 1988); and the role of drift in community colonisation (Boothroyd & Dickie 1991).

The purpose of the present study was to examine: (1) invertebrate drift in five South Island rivers to determine whether diel periodicity of drift in the more common taxa was consistent for a range of river types; (2) drift periodicity for similarity in different life stages or sizes of selected taxa; and (3) the influence of diel drift periodicity on the feeding behaviour of fish.

## STUDY AREAS AND METHODS

### Sampling protocol

Drift was collected over 24 h in each of four rivers (Hawkins River, Ryton River, Rakaia River, Weydon Burn), and over 17 h in one river (Deep Creek), on different dates between 1986 and 1990 (see Table 1 for locations and sampling dates). Water temperature was measured with mercury thermo-meters whenever drift nets were changed (ranges given in Table 1), and the times of sunrise and sunset were noted. Discharge data for the Hawkins, Ryton, and Rakaia Rivers were provided by the Water Resources Centre, DSIR. We estimated the discharges of Deep Creek and the Weydon Burn from measurements of water depth and velocity recorded at a cross-section of the river near the sampling site.

### Sampling sites

The Hawkins River is a headwater tributary of the Selwyn River in North Canterbury. Sampling was undertaken in the middle reaches where the channel was 4–5 m wide with moderately stable beds and banks of gravel and boulders, and many runs and pools. Riparian growth consisted of matagouri *Discaria toumatou*, *Coprosma* spp., gorse *Ulex europaeus*, broom *Cytisus scoparius*, willows *Salix* spp., *Sorbus aucuparia*, and grasses.

The Ryton River, located in the eastern foothills of the Southern Alps, flows into Lake Coleridge.

Samples were collected immediately upstream of the river delta, where the river is braided; channels were 4–10 m wide, and their beds and banks were composed primarily of gravels and small cobbles. Matagouri, gorse, and grasses provided sparse riparian vegetation.

In the Rakaia River, sampling was carried out at two sites (c. 400 m apart) in a minor ( $< 1.0 \text{ m}^3\text{s}^{-1}$ ) braid near the State Highway 1 bridge. Here the river was extensively braided and the channels were 1–50 m wide. Both sampling sites were physically similar and had substrata composed largely of cobbles and gravels, with a small proportion of sand and silt. Riparian vegetation consisted mainly of lupin *Lupinus* spp., broom, and scattered willow trees.

Deep Creek is a spring-fed, high-country tributary of the Rangitata River. Its substrata were mainly cobbles and gravels. At the sampling site the stream flowed through an area of alluvium bordered by open tussock grassland.

The Weydon Burn is a small tributary of the upper Oreti River in Southland. Its source is in the foothills and the stream drains a predominantly pastoral catchment. Drift was collected from a riffle in the lower reaches of the stream where the channel was 4–7 m wide and substrates were primarily small cobbles and gravels. Riparian vegetation was primarily grasses interspersed with patches of tussock and scrub.

### Sampling equipment

Drift samples were collected in all rivers with 400  $\mu\text{m}$  mesh nets fitted to plastic samplers (area of each sampler =  $58.0 \text{ cm}^2$ ), as described by Field-Dodgson (1985). Three replicate samplers were placed in each river immediately below a riffle for 24 h (17 h in Deep Creek). Water depth at all sites was  $< 1.0 \text{ m}$ . The samplers were set so that the top of the net opening just emerged from the water. Intervals at which nets were emptied varied between once an hour around sunrise and sunset in the Hawkins and

**Table 1** General information about sampling sites. Flow data and water temperatures were recorded during each of the sampling periods.

River	Latitude (S)	Longitude (E)	Sampling dates	No. of sets of samples in sampling period	Estimated flow ( $\text{m}^3\text{s}^{-1}$ )	Water temperature ( $^{\circ}\text{C}$ )
Hawkins	42°23'	171°48'	17–18 Dec 86	10	0.1	13.5–19.8
Ryton	43°19'	171°31'	13–14 Jan 87	7	1.2	13.0–20.2
Rakaia	43°44'	172°03'	11–12 Nov 86	11	110	12.5–18.5
Deep Creek	43°33'	170°54'	11–12 Apr 90	4	3.5	8.0–10.5
Weydon Burn	45°35'	168°05'	31 Jan–1 Feb 90	10	$< 0.1$	11.0–23.9

Rakaia Rivers and Weydon Burn, and about once every 9 h in the Ryton River and Deep Creek.

Water velocity readings were taken within the mouth of each net using a Pygmy current meter at the start of each sampling interval and total water flow through each net was calculated from this and the area of submerged net mouth. Samples were preserved in 4% formalin. In the laboratory, invertebrates in each sample were identified to species whenever possible and counted. Head capsule widths of invertebrates which occurred in sufficient numbers (> 100) during day or night samples were measured to the nearest 0.05 mm with an eyepiece micrometer.

### Statistical analysis

Nocturnal drift density (numbers drifting per 100 m<sup>3</sup>) in each river was calculated from the average of all night-time collections. Likewise, diurnal drift density was calculated from the average of all day-time collections. Drift densities from each river were then transformed ( $\log_{10} n + 1$ ) and analysed separately with one-way ANOVA (Sokal & Rohlf 1981). Differences in size frequency distributions of the commoner taxa between day and night were tested for statistical significance with the Kolmogorov-Smirnov two-sample test (Siegel 1956).

## RESULTS

*Deleatidium* spp. (Ephemeroptera) comprised a large proportion of the drift in all rivers, except for the Ryton River, where the Chironomidae (Diptera) was the dominant taxon (Table 2). Other taxa comprising a large proportion of the drift were *Olinga feredayi* (McLachlan) (Trichoptera), *Austrosimulium* spp.

(Diptera), and Chironomidae in the Hawkins River; Chironomidae in the Rakaia River and Deep Creek; and *Hydora* spp. (Coleoptera) in the Weydon Burn. The number of taxa in the drift was greatest in the Weydon Burn and lowest in the Rakaia River (Table 2).

A diel cycle of drift density was evident in all the rivers, except Deep Creek, but the timing of the cycle varied between rivers (Fig. 1). A single night-time peak was recorded during the early evening in the Hawkins River and Weydon Burn (Fig. 1), but in the Rakaia River (Site B) the peak occurred just before sunrise. Peaks at dusk and late morning were recorded in the Ryton River. In the Rakaia River (Site A), drift density peaked during the day (morning and afternoon) and night (just after sunset and just before sunrise). Although drift density appeared to be greater at night than during the day in Deep Creek, the sampling periods at this site were too long for any peaks to be discerned and did not extend over 24 h.

### Drift periodicity and size by taxon

#### *Deleatidium* spp. (Ephemeroptera)

Large numbers of *Deleatidium* spp. were collected from all rivers, except the Ryton (Table 2). Drift density was greater at night than during the day in all rivers, although this was not significant in the Ryton River or Deep Creek (Table 3). In the Hawkins River, Deep Creek, and Weydon Burn, the drift density of this taxon peaked by 2300 h and then decreased throughout the rest of the night (Fig. 1). At the two sites in the Rakaia River, however, although drift density increased immediately after dark, it did not peak until about 0400 h, just before sunrise. At all sites, with the exception of Deep Creek where densities

**Table 2** Percentages of numerical abundance of the most common invertebrate taxa in the total aquatic drift (all samples combined) of five South Island rivers. —, not present. *N* = total number of organisms collected in drift samples.

Taxon	Hawkins ( <i>N</i> = 1346)	Ryton ( <i>N</i> = 1739)	Rakaia (both sites combined) ( <i>N</i> = 9010)	Deep Creek ( <i>N</i> = 7333)	Weydon Burn ( <i>N</i> = 5170)
<i>Deleatidium</i> spp.	15.0	1.8	34.7	68.0	34.2
<i>Nesameletus</i> spp.	0.5	—	—	0.3	4.2
<i>Aoteapsyche</i> spp.	0.5	1.0	14.4	0.1	1.1
Hydrobiosidae	1.6	2.0	14.0	1.5	2.3
<i>Oxyethira albiceps</i>	—	5.3	—	0.9	3.7
<i>Pycnocentroides</i> spp.	6.6	0.5	—	1.1	4.9
<i>Olinga feredayi</i>	32.9	0.6	—	—	4.2
<i>Hydora</i> spp.	0.5	—	—	—	29.5
<i>Austrosimulium</i> spp.	14.3	7.7	0.1	1.2	0.9
Chironomidae	14.8	75.7	35.3	16.5	8.5

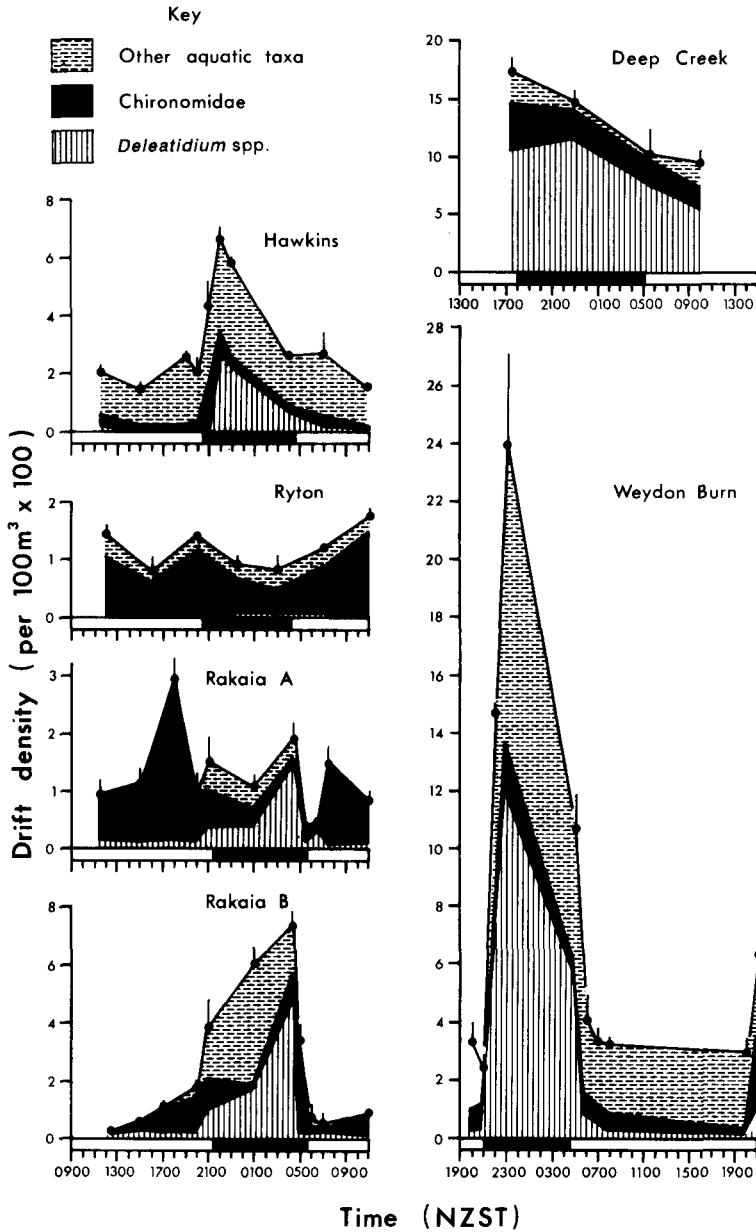


Fig. 1 Density (numbers per 100 m<sup>3</sup>) of total aquatic drift (●) and drift of *Deleatidium* spp. and chironomids in five New Zealand rivers. Vertical lines represent + standard error of the mean (SEM) of total drift. Time from sunset to sunrise is indicated by the black bar along the x-axis.

of up to 1050 per 100 m<sup>3</sup> occurred (Fig. 1), there was relatively little drift of *Deleatidium* spp. during the day.

Insufficient *Deleatidium* spp. from the Ryton River prevented useful analysis of size frequencies. Size frequency plots of *Deleatidium* spp. head capsule widths from the Hawkins and Rakaia Rivers, Deep Creek, and Weydon Burn (Fig. 2) show that although the size range was similar in each river, the populations

were dominated by different life history stages. This was most noticeable in Deep Creek, where the population was dominated by early (< 1.00 mm head width) instar larvae. In contrast, late (> 1.00 mm head width) instars were well represented in the other three rivers. In all rivers except the Hawkins, the mean size of *Deleatidium* spp. drifting at night was greater than during the day, although the difference was not significant ( $P > 0.05$ ) in the Weydon Burn

**Table 3** Mean drift density (numbers per 100 m<sup>3</sup>) during day and night in five South Island rivers. Significant differences between day and night densities (one-way ANOVA on log<sub>10</sub> (n + 1) transformed data) are also shown; \* P < 0.05; \*\* P < 0.01; \*\*\* P < 0.001; NS, not significant; –, not collected.

Taxon	Site: Hawkins		Ryton		Rakaia (both sites combined)		Deep Creek		Weydon Burn	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
<i>Deleatidium</i> spp.	8.8	181.4***	1.4	3.7 NS	10.8	203.5***	803.6	939.0 NS	39.1	801.8***
<i>Nesameletus</i> spp.	1.0	4.4 NS	–	–	–	–	1.2	4.2*	2.8	105.3***
<i>Aoteapsyche</i> spp.	1.0	6.7 NS	1.2	2.4 NS	3.3	69.9***	2.0	0.7 NS	3.2	21.0***
Hydrobiosidae	3.1	9.1*	1.7	3.1 NS	1.8	88.2***	18.9	19.8 NS	3.9	46.2***
<i>Oxyethira albiceps</i>	–	–	6.5	5.1 NS	–	–	11.3	10.2 NS	42.0	84.9*
<i>Pycnocentrodes</i> spp.	22.7	–	0.5	0.7 NS	–	–	21.3	12.3 NS	21.0	22.3 NS
<i>Olinga feredayi</i>	70.5	125.8***	0.3	1.5 NS	–	–	–	–	26.4	53.4*
<i>Hydora</i> spp. – larvae	2.1	2.6 NS	–	–	–	–	–	–	49.6	338.3***
– adults	–	–	–	–	–	–	–	–	51.4	52.7 NS
<i>Austrosimulium</i> spp.	36.2	45.9 NS	11.9	6.1*	0.1	0.0 NS	18.0	16.0 NS	12.2	13.0 NS
Chironomidae – larvae	9.8	22.6 NS	13.4	5.6 NS	11.1	5.7 NS	246.2	131.9**	94.2	150.8*
– pupae	22.7	29.7 NS	89.9	48.8*	76.3	32.3**	38.1	34.9 NS	8.4	32.6*

**Table 4** Mean size (head width) of six aquatic insect taxa taken in day and night drift samples. Results of Kolmogorov-Smirnov two-sample tests comparing size distributions are also shown.

Taxon	River	Mean size (mm)			P
		Day	Night	D <sub>max</sub>	
<i>Deleatidium</i> spp.	Hawkins	1.26	1.06	25.8	> 0.10
	Rakaia A	0.73	1.10	47.0	< 0.001
	Rakaia B	0.92	1.18	33.2	< 0.001
	Deep Creek	0.50	0.55	17.1	< 0.001
	Weydon Burn	0.91	0.94	11.6	> 0.10
<i>Nesameletus</i> spp.	Weydon Burn	0.80	0.91	16.5	> 0.10
<i>Aoteapsyche</i> spp.	Rakaia A	0.92	0.63	48.1	< 0.01
	Rakaia B	0.50	0.56	11.3	> 0.10
<i>Hydrobiosis frater</i>	Rakaia A	0.62	0.93	52.1	< 0.001
	Rakaia B	0.80	0.82	19.2	> 0.10
Hydrobiosidae	Deep Creek	0.55	0.57	8.2	> 0.10
<i>Austrosimulium</i> spp.	Hawkins	0.38	0.41	15.6	> 0.10
	Deep Creek	0.38	0.40	8.1	> 0.10

(Table 4). In the Hawkins River, although the mean size was greater during the day than at night, the difference was not significant.

*Nesameletus* spp. (Ephemeroptera)

Samples collected from the Hawkins River, Deep Creek, and Weydon Burn contained sufficient individuals for analysis of drift periodicity (Table 2). In these three rivers, the mean drift density was greater at night than during the day, although the difference was not significant in the Hawkins River (Table 3). In the Hawkins River and Weydon Burn, peak abundance was at 2200 h (Fig. 3). Sufficient individuals for an analysis of size differences were collected only from the Weydon Burn where, although the frequency of most size classes increased at night,

the mean sizes at night and day were similar (Table 4). Late instars (> 1.2 mm head width) were not collected in the drift during the day.

*Aoteapsyche* spp. (Trichoptera)

These net-spinning caddisflies, primarily *A. tepoka* (Mosely), *A. colonica* (McLachlan), and *A. raruraru* (McFarlane) were collected in low numbers from all rivers (Table 2). With the exception of Deep Creek, where they comprised the smallest proportion of the drift, their density was greater at night than during the day (Table 3). However, the differences were significant only in the Rakaia River and Weydon Burn. In the Rakaia River, peak abundance occurred at 2100 h at Site A and 0100 h at Site B (Fig. 3). Analyses of *Aoteapsyche* spp. sizes were restricted to

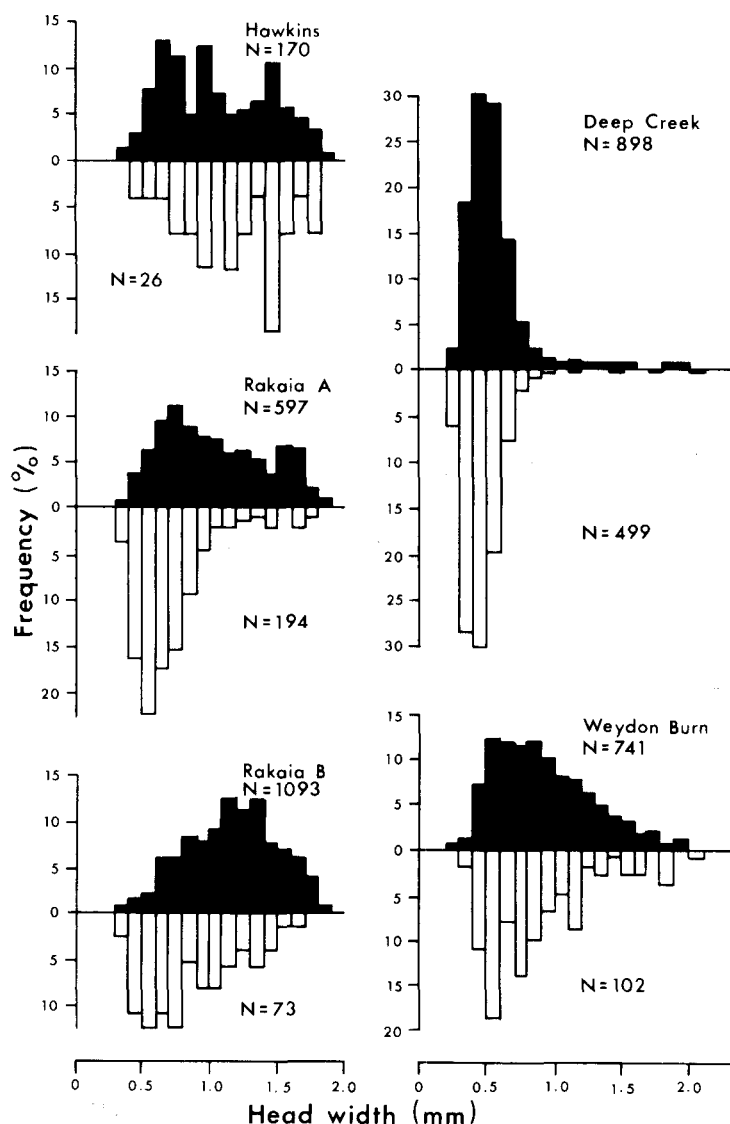


Fig. 2 Length frequencies of head capsule widths of *Deleatidium* spp. collected from the drift in four New Zealand rivers during night (shaded) and day (open).

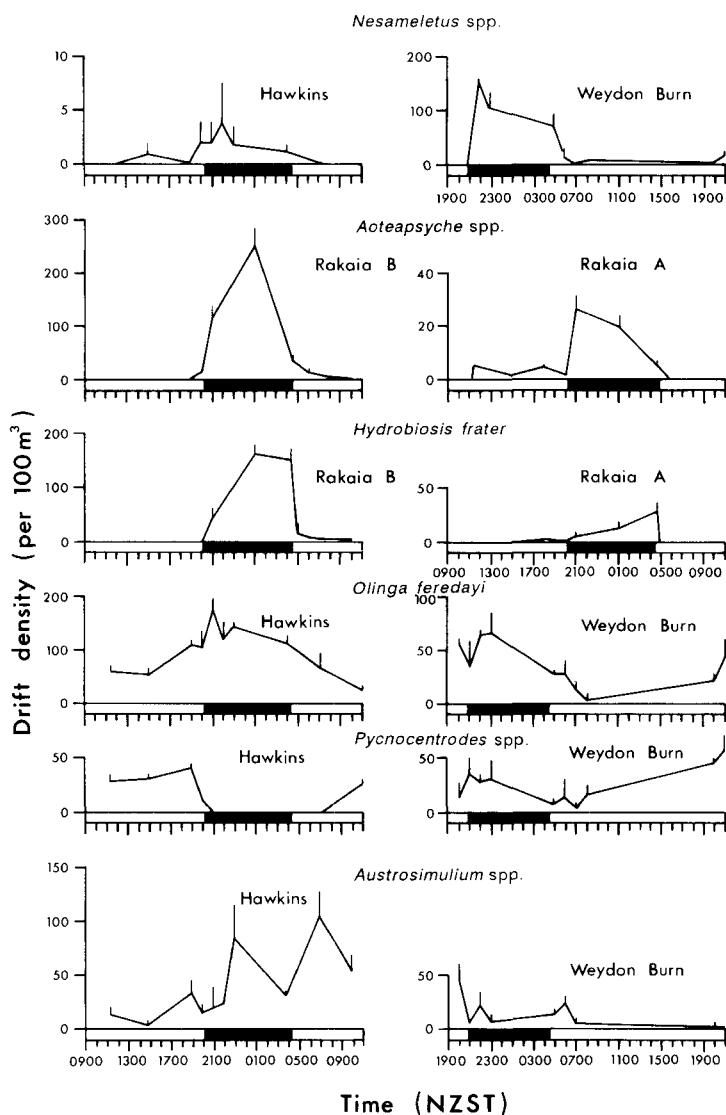
the two sites in the Rakaia River, where third to fifth instar larvae (as defined by Crosby 1975) occurred in the drift; mean size was greater by day than by night at Site A and the difference was not significant at Site B. However, relatively few individuals of any size drifted during the day compared to those drifting at night (Table 3, Fig. 4).

### Hydrobiosidae (Trichoptera)

In the Rakaia River, this taxon was represented only by *Hydrobiosis frater* McLachlan, but in the other rivers it included species of *Hydrobiosis*, *Costachorema*, and *Psilochorema*, none of which occurred

in sufficient numbers to be analysed separately. Drift density was greater at night than in the day in all rivers, although differences were not significant in the Rytton River or Deep Creek (Table 3). At the two sites in the Rakaia River, drift density of *H. frater* peaked by 0100 h at Site B and by 0430 h at Site A (Fig. 3), whereas that of Hydrobiosidae in the Weydon Burn peaked by 2200 h. The size range of *H. frater* drifting in the Rakaia River was similar during the day and night (Fig. 4), although few larvae were collected during the day. Larger *H. frater* drifted during the night at Site A in the Rakaia River, but sizes were similar during day and night at Site B

**Fig. 3** Density (numbers per 100 m<sup>3</sup>) of selected taxa collected from the drift over 24 h in three New Zealand rivers. Vertical lines represent + SEM. Time from sunset to sunrise is indicated by the black bar along the x-axis.



(Table 4). In Deep Creek, small Hydrobiosidae drifted during the day and night (Table 4).

#### *Oxyethira albiceps* (McLachlan) (Trichoptera)

The abundance of this species was similar during day and night in the Ryton River and Deep Creek, but it was more abundant at night in the Weydon Burn (Table 3).

#### *Olinga feredayi* (McLachlan) (Trichoptera)

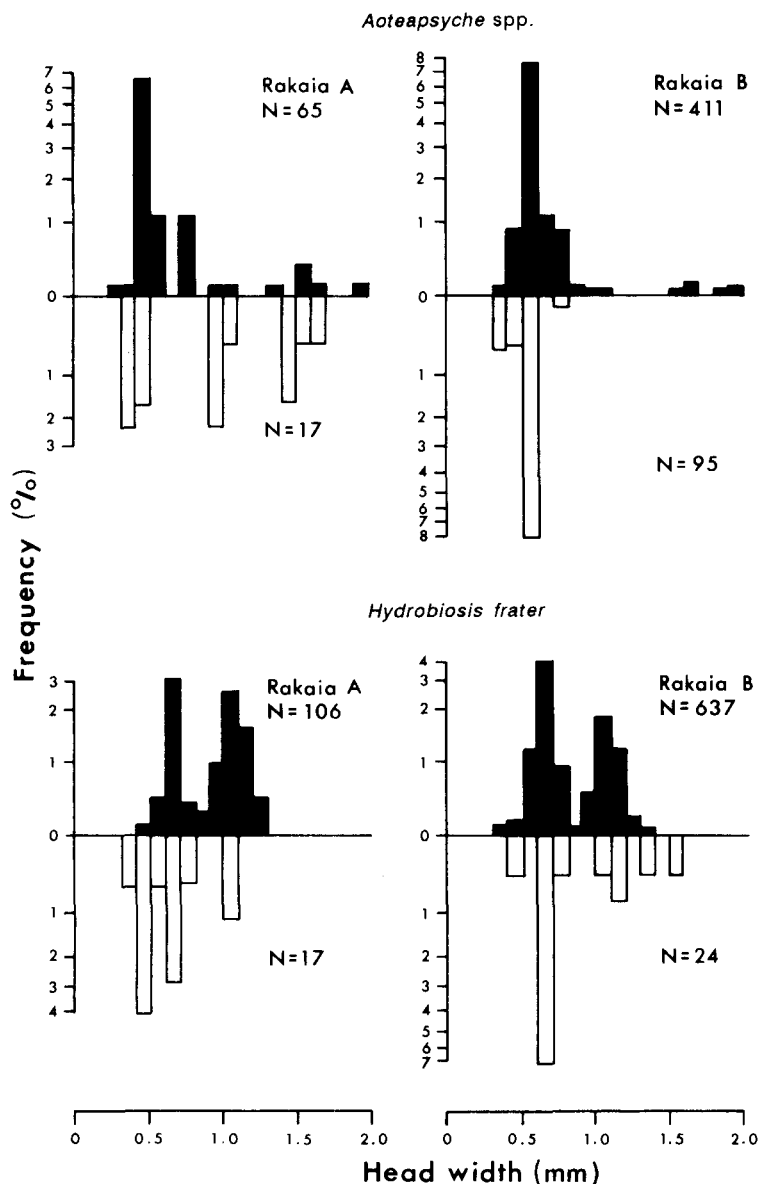
Significantly more *O. feredayi* drifted at night than during the day, with peak abundance occurring 1–2 h

after sunset in both the Hawkins River and Weydon Burn (Table 3, Fig. 3). However, although more drift occurred at night, relatively high densities were also recorded during the day (Fig. 3).

#### *Pycnocentroides* spp. (Trichoptera)

This taxon had a well-defined diurnal drift pattern in the Hawkins River, but not in the Ryton River, Deep Creek, and Weydon Burn, where the differences between drift density during the day and night were not significant (Table 3). In the Hawkins River, abundance peaked about an hour before sunset and

Fig. 4 Length frequencies of head capsule widths of selected aquatic taxa collected from the drift during night (shaded) and day (open).



then declined rapidly, such that no larvae were collected in the drift at night (Fig. 3). In the Weydon Burn, peak abundance was at sunset and lowest numbers were collected 2–3 h after sunrise the following day (Fig. 3).

#### *Hydora* spp. (Coleoptera)

In the Weydon Burn, *Hydora* larvae drifted significantly more at night than during the day, but

densities of adults collected during day and night were similar (Table 3).

#### *Austrosimulium* spp. (Diptera)

*Austrosimulium* drift densities were similar during day and night in all but the Ryton River, where larvae drifted significantly more during the day than at night (Table 3). Plots of drift density over 24 h in the Hawkins River and Weydon Burn (Fig. 3) showed



large fluctuations, particularly pre- and post-sunset and shortly after sunrise. The size distributions of *Austrosimulium* spp. drifting in the Hawkins River were similar during day and night (Table 4).

### Chironomidae (Diptera)

Chironomid larvae showed no general pattern of drift periodicity in all rivers. In the Ryton and Rakaia Rivers and Deep Creek, their densities were greater during the day than at night, but the difference was only significant in Deep Creek (Table 3). Densities were greater at night than during the day in the Hawkins River and Weydon Burn, although the difference was only significant in the Weydon Burn (Table 3). At Site A in the Rakaia River, there were peaks of abundance at 1800 and 2100 h, but at other times and in all other rivers, drift density was relatively uniform (Fig. 1). The drift periodicity of chironomid pupae in the drift was similar to that of the larvae, with significantly more occurring during the day than at night in the Ryton and Rakaia Rivers and fewer during the day than at night in the Weydon Burn (Table 3). In the Ryton and Rakaia Rivers, the drift density of chironomid pupae peaked shortly before sunset and after sunrise.

### DISCUSSION

Drift in most lotic systems increases rapidly soon after sunset (Waters 1972). Our study, and those of McLay (1968), Watson (1971), Cadwallader (1975), Death (1988), and Graesser (1988) show that New Zealand streams generally are no exception in this respect. However, drift peaks were evident around sunset and sunrise in the Manganuiateao River during May and October (Collier & Wakelin in press).

In our study, post-dusk increases in drift density were particularly marked in the Hawkins and Rakaia Rivers and in the Weydon Burn. The lack of a marked post-dusk increase in drift density in the Ryton River and Deep Creek may be explained by the composition of the drift in these rivers. The composition of drift in the Ryton River differed from that of all other streams investigated in that most invertebrates collected were chironomids which did not exhibit any marked diel periodicity in drift density. Their dominance and the low density of other taxa meant that no marked diel pattern of periodicity was evident in the total drift. The tendency to drift at night increases with size for the mayflies *Cinygmula* sp. and *Baetis tricaudatus* in North American streams, behaviour which has been described as a means of avoiding predation by fish

(Allan 1984; Skinner 1985). In New Zealand, larger *Deleatidium* also have a propensity to drift at night (Devonport & Winterbourn 1976; Sagar & Glova in press, this study). However, in Deep Creek, small *Deleatidium* greatly outnumbered large individuals, so even a marked increase in the number of larger *Deleatidium* would not have a noticeable effect on the total drift density.

The general pattern of drift across a range of river types appears to be consistent for *Deleatidium* spp., *Coloburiscus humeralis* (Walker), *Aoteapsyche* spp., and *Olinga feredayi*, all of which are generally night-active (Table 5). Numerous Northern Hemisphere (e.g., Elliott 1968; Kohler 1983; Allan et al. 1986) and Australian (e.g., Bailey 1981; Graesser & Lake 1984) studies indicate that most mayflies and free-living caddisflies are generally night-active in the drift, so it is not surprising to find the same trends within these groups in New Zealand. Day-active drift appears to be general for *Pycnocentropes* spp. and *Beraeoptera roria* Mosely (Table 5).

The diel periodicity of other taxa in the drift is not as clear and some of this variation is presumably because more than one species was involved. Although we found *Nesameletus* spp. were night-active in the three rivers where collected, Cadwallader (1975) found they occurred in the drift throughout 24 h in the Glentui River. Hydrobiosidae were night-active in six rivers and day-active in one river (Table 5). *Pycnocentropes* spp. was strongly day-active in the drift of a Waitakere stream (Watson 1971), the Cave Stream (Death 1988), and the Glentui (Cadwallader 1975), Manganuiateao (Collier & Wakelin, in press), and Hawkins (this study) Rivers, but occurred throughout the day and night in Deep Creek and the Weydon Burn. The adults of elmids (*Hydora* spp.) can be night-active (Watson 1971; this study), day-active (McLay 1968; Cadwallader 1975), or their densities in the drift may be similar during both day and night (this study). The occurrence of chironomid larvae and pupae in the drift is also variable, with maximum densities being reported during both day and night (Watson 1971; Cadwallader 1975; this study).

In the clear-water Glentui and Hawkins Rivers, Deep Creek, and Weydon Burn, there was the expected peak of abundance in the drift density of *Deleatidium* spp. shortly after sunset (Cadwallader 1975; this study). However, in the more turbid glacier-fed Rakaia River, the drift density of *Deleatidium* increased rapidly at sunset and peaked shortly before sunrise. *Deleatidium* is a morphologically highly variable genus and the populations in the rivers

**Table 5** Summary of several New Zealand drift studies in different rivers, showing taxa which exhibited marked diurnal or nocturnal drift periodicities.

Reference	Location	Taxon with marked drift periodicity	
		Diurnal	Nocturnal
McLay 1968	Kakanui River, Otago	Oligochaetes Chironomidae Elmidae	<i>Deleatidium</i> Hydrobiosidae
Watson 1971	Waitakere stream, Auckland	<i>Pycnocentroides</i> <i>Beraeoptera</i> Chironomidae	<i>Deleatidium</i> <i>Zephlebia</i> <i>Zelandoperla</i> <i>Aoteapsyche</i> Elmidae
Cadwallader 1975	Glentui River, Canterbury	<i>Pycnocentroides</i> <i>Beraeoptera</i> Chironomidae Elmidae	<i>Deleatidium</i> <i>Zephlebia</i> <i>Coloburiscus</i> <i>Aoteapsyche</i> Hydrobiosidae <i>Olinga</i> <i>Pycnocentria</i>
Fechney 1988	Dalgety Stream, Canterbury	<i>Pycnocentria</i> Chironomidae Empididae	<i>Deleatidium</i> <i>Olinga</i> Tipulidae
Death 1988	Cave Stream, Canterbury	<i>Pycnocentroides</i>	<i>Deleatidium</i> Hydrobiosidae
Graesser 1988	Westland streams		<i>Deleatidium</i>
Collier & Wakelin in press	Manganuiateao River, central North Island	<i>Hydrobiosidae</i> <i>Pycnocentroides</i> <i>Beraeoptera</i> <i>Helicopsyche</i> Chironomidae	<i>Coloburiscus</i>
This study	Hawkins River, Canterbury		<i>Deleatidium</i> Hydrobiosidae <i>Olinga</i>
This study	Ryton River, Canterbury	Chironomidae <i>Austrosimulium</i>	
This study	Rakaia River, Canterbury	Chironomidae	<i>Deleatidium</i> <i>Aoteapsyche</i> Hydrobiosidae
This study	Deep Creek, Canterbury	Chironomidae	<i>Nesameletus</i>
This study	Weydon Burn, Southland		<i>Deleatidium</i> <i>Nesameletus</i> <i>Aoteapsyche</i> Hydrobiosidae <i>Oxyethira</i> <i>Olinga</i> Elmidae Chironomidae

sampled in our study belonged to the informal *lilli* and *myzobranchia* groups (Winterbourn & Gregson 1989), so several species are involved. Different species of *Deleatidium* may occur in clear-water and glacier-fed lotic systems and this may explain the

differences in diel timing of peak abundance in the drift. Alternatively, differences in the time of year samples were collected, size distributions of larvae present, or predation pressures may have modified the behaviour of the mayflies.

Comparisons of night versus day size composition of drift showed that only for *Deleatidium* were larger individuals generally more common in the drift at night than during the day. This aspect of its behaviour is shared by several other mayfly species, see e.g., Elliott 1968; Allan 1984; Skinner 1985. The differences in size were even significant in Deep Creek, where larvae were predominantly small. The apparently unusual situation in the Hawkins River, where the mean size of drifting *Deleatidium* was greater during the day than at night, is probably best explained by the small sample size collected during the day; the small size resulted in a relatively low number of large individuals having a large influence on the size composition. Despite a wide range of size classes occurring among drifting *Aoteapsyche* spp. and Hydrobiosidae, night-day differences even within the same river (Sites A and B in the Rakaia) were not consistent, although the small number of animals collected during the day could have biased the results.

*Deleatidium*, *Nesameletus*, *Aoteapsyche*, Hydrobiosidae, and Chironomidae are widely distributed in lotic systems in New Zealand (Winterbourn & Gregson 1989). Several species of fish feed, at least in part, on drifting invertebrates and some selectively prey upon larger *Deleatidium* (Sagar & Glova 1987, 1988; Glova & Sagar 1989). The extent to which fish may feed selectively to some extent depends upon the availability of prey. The present study shows that the diel periodicity of drifting invertebrates and the occurrence of larger instars of *Deleatidium* in the drift is generally consistent across a range of stream types. Such patterns of prey abundance may influence the behaviour of fish which feed predominantly on drifting invertebrates. For example, in the Glentui and Hawkins Rivers, the peak in feeding of the common river galaxias *Galaxias vulgaris* coincided with the period of abundant drift after dusk (Cadwallader 1975; Glova & Sagar 1989). However, not all fish species are able to feed throughout the night, so they may be limited to feeding when invertebrate drift is scarcer.

#### ACKNOWLEDGMENTS

We thank Marty Bonnett, Colin Docherty, Ingemar Näslund, Nigel Smith, and Trevor Washbourne for field assistance, and Louise Clarke, Garry Scrimgeour, and Nigel Smith for laboratory assistance in sorting the invertebrates samples. We are grateful to Kevin Collier, Brendan Hicks, Mike Winterbourn, and an anonymous reviewer for helpful reviews of earlier drafts of the manuscript.

#### REFERENCES

- Allan, J. D. 1984: The size composition of invertebrate drift in a Rocky Mountain stream. *Oikos* 43: 68–76.
- Allan, J. D.; Flecker, A. S.; McClintock, N. L. 1986: Diel epibenthic activity of mayfly nymphs, and its nonconcordance with behavioral drift. *Limnology and oceanography* 31: 1057–1065.
- Bailey, P. C. E. 1981: Diel activity patterns in nymphs of an Australian mayfly *Atalophlebiodes* sp. (Ephemeroptera: Leptophlebiidae). *Australian journal of marine and freshwater research* 32: 121–131.
- Boothroyd, I. K. G.; Dickie, B. N. 1991: Macroinvertebrate drift and community colonisation on perspex artificial substrates in the Ohinemuri River, New Zealand. *New Zealand journal of marine and freshwater research* 25: 167–176.
- Brittain, J. E.; Eikeland, T. J. 1988: Invertebrate drift: a review. *Hydrobiologia* 166: 77–93.
- Burnet, A. M. R. 1969: A study of the inter-relation between eels and trout, the invertebrate fauna and the feeding habits of the fish. *New Zealand Marine Department fisheries technical report* 36. 12 p.
- Cadwallader, P. L. 1975: Feeding habits of two fish species in relation to invertebrate drift in a New Zealand river. *New Zealand journal of marine and freshwater research* 9: 11–26.
- Collier, K. J.; Wakelin, M. D. in press: Drift of aquatic macroinvertebrate larvae in Manganuiateao River, central North Island. *New Zealand journal of natural sciences*.
- Crosby, T. K. 1975: Food of the New Zealand trichopterans *Hydrobiosis parumbripennis* McFarlane and *Hydropsyche colonica* McLachlan. *Freshwater biology* 5: 105–114.
- Death, R. G. 1988: Drift distance, periodicity and frequency of benthic invertebrates in a cave stream. *Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie* 23: 1446–1550.
- 1989: The effect of a cave on benthic invertebrate communities in a South Island stream. *New Zealand journal of natural sciences* 16: 67–78.
- Devonport, B. F.; Winterbourn, M. J. 1976: The feeding relationships of two invertebrate predators in a New Zealand river. *Freshwater biology* 6: 167–176.
- Elliott, J. M. 1968: The daily activity patterns of mayfly nymphs (Ephemeroptera). *Journal of zoology* 155: 201–221.
- Fechney, L. R. 1988: The summer diet of brook trout (*Salvelinus fontinalis*) in a South Island high-country stream. *New Zealand journal of marine and freshwater research* 22: 163–168.

- Field-Dodgson, M. S. 1985: A simple and efficient drift sampler. *New Zealand journal of marine and freshwater research* 19: 167–172.
- Glova, G. J.; Sagar, P. M. 1989: Prey selection by *Galaxias vulgaris* in the Hawkins River, New Zealand. *New Zealand journal of marine and freshwater research* 23: 153–161.
- 1991: Dietary and spatial overlap between stream populations of a native and two introduced fish species in New Zealand. *Australian journal of marine and freshwater research* 42: 423–433.
- Graesser, A. K. 1988: Invertebrate drift in three flood-prone streams in South Westland, New Zealand. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* 23: 1422–1426.
- Graesser, A.; Lake, P. S. 1984: Diel changes in the benthos of stones and of drift in a southern Australian upland stream. *Hydrobiologia* 111: 153–160.
- Kohler, S. L. 1983: Positioning on substrates, positioning changes, and diel drift periodicities in mayflies. *Canadian journal of zoology* 61: 1362–1368.
- Irvine, J. R.; Henriques, P. R. 1984: A preliminary investigation on effects of fluctuating flows on invertebrates of the Hawea River, a large regulated river in New Zealand. *New Zealand journal of marine and freshwater research* 18: 283–290.
- McLay, C. L. 1968: A study of drift in the Kakanui River, New Zealand. *Australian journal of marine and freshwater research* 19: 139–149.
- 1970: A theory concerning the distance travelled by animals entering the drift of a stream. *Journal of the Fisheries Research Board, Canada* 27: 359–370.
- Müller, J. 1974: Stream drift as a chronological phenomenon in running water ecosystems. *Annual review of ecology and systematics* 5: 309–323.
- Sagar, P. M.; Glova, G. J. 1987: Prey preferences of a riverine population of juvenile chinook salmon *Oncorhynchus tshawytscha*. *Journal of fish biology* 31: 661–673.
- 1988: Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile chinook salmon *Oncorhynchus tshawytscha*. *Journal of fish biology* 33: 643–653.
- in press: Invertebrate drift in a large, braided New Zealand river. *Freshwater biology*.
- Siegel, S. 1956: Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill. 312 p.
- Skinner, W. D. 1985: Night-day drift patterns and the size of larvae of two aquatic insects. *Hydrobiologia* 124: 283–285.
- Sokal, R. R.; Rohlf, F. J. 1981: Biometry. 2nd ed. San Francisco, Freeman.
- Statzner, B.; Dejoux, C.; Elouard, J. M. 1984: Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast). I. Introduction: a review of drift literature, methods, and experimental conditions. *Revue d'hydrobiologie tropicale* 17: 319–334.
- Waters, T. F. 1972: The drift of stream insects. *Annual review of entomology* 17: 253–272.
- Watson, G. W. 1971: Drift of stream invertebrates. *Tane* 17: 197–212.
- Winterbourn, M. J.; Gregson, K. L. D. 1989: Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand* 9. 96 p.