

Long-term patterns of invertebrate stream drift in an Australian temperate stream

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SUMMARY

1. Invertebrate stream drift was sampled bimonthly in the Acheron River, Victoria, Australia, over a period of 18 months. Replicated hourly samples were collected over a 25-h period on each sampling date. A total of 194 taxa were identified in the drift. However, total drift density was dominated by few taxa.
2. Some evidence was obtained for a seasonal pattern in drift: this was most pronounced in relative abundances of individual taxa and the composition of the drift, rather than in total drift densities. Most of the commonly collected taxa reflected the seasonal pattern of total drift. However, some of the common taxa did not.
3. A small number of taxa showed behavioural drift, with a nocturnal increase in drift densities. One species of '*Baetis*' drifted in high densities over short periods of time around dusk and dawn. It did not drift in higher densities during the night than during the day. The results emphasize the need for drift studies to be more rigorously designed than is typically the case.

Introduction

Invertebrate drift is a common phenomenon in streams and has been considered important to stream ecosystems for a variety of reasons. It provides a mechanism for colonizing disturbed areas or supplying a food resource for other animals (for reviews of drift refer to Waters, 1972; Müller, 1974; Statzner, Dejoux & Elouard, 1984; Brittain & Eikeland, 1988).

Different types of drift have been described on the basis of patterns in drift densities over 24 h (Waters, 1972). The three major types that are commonly described in the literature are constant drift, behavioural drift and catastrophic drift (Waters, 1972). Constant drift involves low and irregular densities and is thought to be due to the accidental displacement of individuals from the stream bottom (Watson, 1971; Waters, 1972). Catastrophic drift is defined as the drift resulting from major physical disturbances of the benthos, such as those caused by floods or pesticide applications (Rae, 1987; Wallace *et al.*, 1987). Behavioural drift has received most attention in ecological studies because it is thought to be the result of some diel behavioural pattern of the individuals involved (Waters, 1965). Often densities

increase at night, and this has led to speculation about the evolution of behavioural drift as a predator avoidance mechanism (Allan, 1978; Flecker, 1992).

The description of diel patterns, however, is often based on the subjective interpretation of graphs of drift density with time, as often only one sample has been collected per time period (Brittain & Eikeland, 1988). Because of this, differences between time periods can not be tested objectively. Night and day drift has been compared by treating consecutive samples collected during the night (or day) as replicates and then testing for differences between day and night (Benson & Pearson, 1987). However, samples in adjacent time periods may not be independent of each other, and thus a basic statistical assumption is violated (Manly, 1992). When replicate drift samples are collected, these are often taken over a short period (e.g. 1 h) within a longer time period (e.g. 3 h). The samples taken during the day and the night, respectively, are pooled and the difference between night and day samples is tested for (Allan, 1978; Poff, DeCino & Ward, 1991; Flecker, 1992). However, it has been argued that peaks in drift can occur over short periods, such as 1 h or less, and thus sampling intermittently over a 24-h period could mean that some

peaks in drift densities are missed (Elliott, 1969). Thus, whilst many descriptive studies of drift have been published, the design of drift studies, and analyses of patterns, remain problematic.

Drift also varies over longer time periods, such as seasons (Brittain & Eikeland, 1988). However, due to the number of samples needed to describe diel patterns in drift (Elliott, 1969), many studies have been short term, and few have described seasonal changes in diel patterns (Brittain & Eikeland, 1988). Rigorous, comprehensive studies investigating both short- and long-term changes in composition and density of drift are rare (and absent for temperate Australia) and represent a gap that this study aims to fill.

In particular, this study wanted to answer four questions.

- Which benthic invertebrate taxa can be collected in the drift in an Australian temperate stream?
- How does the composition and density of drift change on a seasonal basis?
- Do invertebrate taxa in an Australian temperate stream show behavioural drift?
- Do diel drift patterns vary seasonally?

Materials and Methods

The study site lay in an undisturbed, upland section of the Acheron River, 10 km north of Warburton (145°43'E, 37°38.5'N), in southern Victoria, Australia. Annual peak discharge of the Acheron River was 5368 megalitres/day in August, 1981, and 932 megalitres/day in June, 1982 (Rural Water Cooperation of Victoria). The unusually low discharge in 1982 reflected the drought in Victoria at that time (Bureau of Meteorology, Victoria, Melbourne). During the study, the pH of the river varied from 5.0 to 7.7 at the study site, and water temperature ranged from 5°C in June 1982 to 15.5°C in February 1983. Diel changes in water temperature were measured in December 1981 and were negligible (2°C) relative to seasonal changes.

Drift was sampled at the downstream end of a 15-m-long riffle, which had an average width of 5 m and an average depth of 0.24 m. The drift samplers designed for this study consisted of two parts described below.

1 A sheet-metal box in the shape of the frustrum of a four-sided pyramid (small opening = 225 cm², large opening = 900 cm², sides = 30 cm), which was fixed on metal rods sunk into the stream bed. The smaller opening faced upstream to reduce clogging and to increase

the efficiency of the net (Elliott, 1970; Muirhead-Thomson, 1987). This was confirmed by observing the flow of dye through the samplers (Field-Dodgson, 1985). This design also allowed for the upstream opening of the sampler to be raised from the bottom of the stream so that invertebrates could enter the sampler only by drifting.

2 An easily removable 2-m-long net with a mesh size of 0.3 mm and a detachable sampling bottle.

Drift samples were collected by quickly removing the net from the sampling box, washing its contents into the sampling bottle, attaching a new sampling bottle and replacing the net on the box.

Drift samples were collected on nine dates over 18 months (four in summer, two in autumn, two in winter and one in spring; Table 1). On each of these dates, drift was sampled hourly for 25 consecutive hours, except on 16 and 17 April, 1983, when drift samples were collected over 24 h. Two drift samples were collected per hour on all occasions, except in December 1981, when three samples were collected per hour.

The drift samplers were placed side-by-side in the central, most turbulent part of the stream, where the action of the current mixes suspended material (Hynes, 1970). It was assumed that this positioning allowed the collection of random, independent, replicate samples of drift during each hour.

All sampling dates were chosen close to a new moon to minimize possible repression of nocturnal drift by moonlight (Ulfstrand, 1968; Casey, 1987). A torch covered with red cellophane was used to work by at night, as red light was thought to have no effect on drifting invertebrates (Elliott, 1968). Recently Heise (1992) published evidence that invertebrates can be sensitive to visible red light. Nevertheless, it was thought unlikely

Table 1 Sampling dates and acronyms used for presentation of results

Acronyms	Actual date of sampling
SUM1a	22 and 23 December 1981
SUM1b	24 and 25 February 1982
SUM2a	16 and 17 December 1982
SUM2b	15 and 16 February 1983
AUT1	26 and 27 April 1982
AUT2	16 and 17 April 1983
WIN1a	24 and 25 June 1982
WIN1b	10 and 11 August 1982
SPR	19 and 20 October 1982

that the light used, whilst clearing the nets, repressed drift, as the design of the samplers allowed for a very quick collection of samples and, overall, minimal use of any light. The area upstream from the samplers, which could have been a potential source of drift, was not illuminated at all.

Current velocity was measured hourly at the mouth of each sampler with a SIAP ME 4001 current meter. Light intensity reflected from a Kodak Neutral Test card, with 18% reflection, held just above each sampler, was measured hourly with a Luna 6III, or a Weston Master, light meter to allow a consistent definition of sunset (= the hour during which light intensity dropped to less than 1 lux) and sunrise (= the hour during which light intensity increased to more than 1 lux).

All samples were preserved in 10% formaldehyde in the field. In the laboratory, arthropods were separated from detritus by a kerosene phase-separation technique (Barmuta, 1984), to ensure that, in particular, small instars of insects, such as chironomids, were picked from samples consistently, despite variations in amounts of detritus collected. Because this technique does not work equally well with non-arthropods as arthropods, the detritus fraction was also examined under the microscope. Whenever possible invertebrates were identified to species or to voucher groups established by the Museum of Victoria. Reference specimens of most taxa were checked by workers with taxonomic experience in the relevant groups (see Acknowledgments).

Analysis

Calculation of drift densities. Drift densities were calculated for each hour and net as number of invertebrates/ m^3 of water passing through the net. The average current velocity measured at the beginning and the end of each sample period was used to calculate discharge. Mean drift densities per date of sampling were calculated by pooling all hourly densities for each net and dividing by the total number of hours sampled at that time.

Seasonal changes in drift. The differences in total drift densities was tested for, as well as differences in drift densities of major invertebrate taxa, with a one-way analysis of variance (ANOVA), followed by Ryan's test, which has been recommended as a powerful *post-hoc* comparison of means test in which the experimental error rate is controlled (Day & Quinn, 1989). The as-

sumptions of normality and variance homogeneity for ANOVA were checked by examining plots of residuals against estimates from the ANOVA. If necessary, the data were transformed to fulfil these assumptions. For Ryan's test the harmonic mean was used, as in Kramer's modification of Tukey's test (Day & Quinn, 1989), because three replicates were taken in December 1981 and two replicates were taken on all subsequent sampling occasions.

Detrended correspondence analysis (Cornell Ecology Program DECORANA; Hill, 1979) was used as an ordination technique to display patterns in the composition and relative abundances of invertebrates in the seasonal drift samples. Sample months were treated equitably by standardizing total drift density for each month to 100, and adjusting individual species densities accordingly. This decreases the influence of common species in the ordination and allows examination of patterns based on all species in the analysis and their abundances relative to each other. Rare species (those represented by three or fewer individuals and present in fewer than 6% of all samples collected per 25-h sample period) were deleted prior to multivariate analysis (Gauch, 1982).

Diel changes in drift

For the examination of diel drift patterns, time series analysis was used. This was believed to be an appropriate, albeit new, approach to the analysis of diel drift, because contiguous samples were taken through time [= definition of a time series (Manly, 1992)] on each sampling date.

A test developed by Finch (1973) for the detection of a change in the level of a short time series following a particular event (= L) was used. Sunset and sunrise were considered to be two events that could potentially change the level of drift. Each collection of twenty-five hourly drift samples was divided into two short time series, and tested for the effects of sunrise and sunset separately: the first time series included all samples taken before sunset and at night; the second time series included all night samples and all samples taken after sunrise.

Initially, all samples in a short time series were ranked. This time series, X , then consisted of a series of ranks, with l ranks occurring before and k ranks occurring after the event L (i.e. $X = l + k$). Ties in ranks were dealt with by a mid-rank method, whereby a rank was allocated to

a tied term by averaging the ranks that these terms would have had if they had been distinguishable. The L -level of the time series $X [= L(X)]$ was defined as the number of the smallest elements of X which occur in the last k places, and the probability $[L_A(X)]$ of this occurring by chance was calculated in the following way:

$$\text{Let } L_A(X) = \Sigma \Omega(c), \text{ where } c = L(X)$$

and

$$\Omega(c) = \binom{k}{c} \binom{l}{k-c} \binom{k+l}{k}^{-1}$$

where $c = (k-l)^+, (k-l)^++1, \dots, k$.

and $(k-l)^+ = \text{Max}(0, k-l)$.

Because $(k-l)^+$ takes on the maximum value of either 0 or $(k-l)$, c will always be a positive number. In addition, c has to be equal to or greater than $L(X)$. For example, if $l = 21$, $k = 7$ and $L(X) = 6$, then c could only take on the values of 6 and 7 (Finch, 1973). Thus, for this example, $\Sigma \Omega(c) = \Omega(6) + \Omega(7)$, and $L_A(X)$ would be equal to 1.25×10^{-4} .

A probability level of $L_A(X) = 0.05$ was used to decide when a significant change in the level of drift occurred at L . If a significant increase in the level of drift occurred at both sunset and sunrise on more than one sampling occasion, the taxon under investigation was classified as exhibiting behavioural drift at these times.

Results

Drift composition

Invertebrate drift was dominated by eleven aquatic taxa, which contributed almost half (43.6%) the total

number of invertebrates collected (Table 2). Terrestrial invertebrates were also collected in the drift nets and contributed 7.9% to total drift (adult Diptera = 2.2%, Hemiptera nymphs = 2.1% and terrestrial mites = 3.6%). Overall, a total of 194 taxa were identified in the drift over the study period (for a complete list of the total number of individuals collected in each taxon see Schreiber, 1988). Sixty taxa were regarded as 'rare' and are not considered further.

Seasonal changes in invertebrate stream drift

Total drift density showed a seasonal pattern with a peak in both summers (Fig. 1, Table 3). However, the peak in total drift was greater and occurred later in the first than the second summer (Fig. 1). A seasonal pattern was also evident when all but the rare taxa were analysed together: based on the relative abundances of drifting taxa on each sampling date, summer samples were closer to each other than to non-summer samples in ordination space (Fig. 2).

Most, but not all common taxa had similar seasonal drift patterns, reflecting that of total drift, with a peak in summer (Appendix 1). However, for some taxa the peak was not repeated in the second summer of the study (Appendix 1). Different seasonal patterns were evident for other common taxa in the drift: *Podonomopsis* sp.1 drifted most in spring, *Riekoperla williamsi* and *Zavreliella* sp.1 tended to drift in higher densities in winter and spring than at other times of the year, and, whilst *Alloecella grisea* and *Illiesoperla australis* showed changes in drift density over the study period, peaks could not be identified clearly (Appendix 1).

Taxon	% of total drift
<i>Zavreliella</i> sp.1 (Diptera: Chironomidae)	7.32
<i>Austrosimulium mirabile</i> Mackerras+Mackerras (Diptera: Simuliidae)	6.59
<i>Nousia</i> sp.A1 (Ephemeroptera: Leptophlebiidae)	4.80
<i>Pseudomoera fontana</i> (Sayce) (Amphipoda: Eusiridae)	4.32
<i>Condocerus paludosus</i> Neboiss (Trichoptera: Leptoceridae)	3.68
'Baetis' sp.MV2 (Ephemeroptera: Baetidae)	3.44
<i>Riekoperla williamsi</i> McLellan (Plecoptera: Gripopterygidae)	2.86
<i>Tanytarsus</i> sp.MV36E (Diptera: Chironomidae)	2.84
<i>Alloecella grisea</i> Banks (Trichoptera: Helicophidae)	2.82
'Baetis' sp.MV3 (Ephemeroptera: Baetidae)	2.70
<i>Hydrobiosella</i> sp. (Trichoptera: Philopotamidae)	2.23
Total	43.60

Table 2 Common aquatic taxa in the drift and their relative contributions to total drift

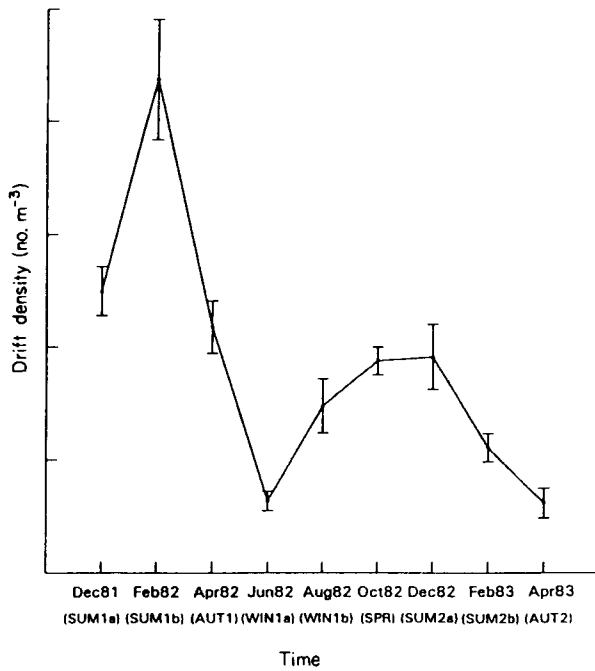


Fig. 1 Seasonal changes in total invertebrate drift density (no m⁻³). Error bars represent the range sampled by the nets.

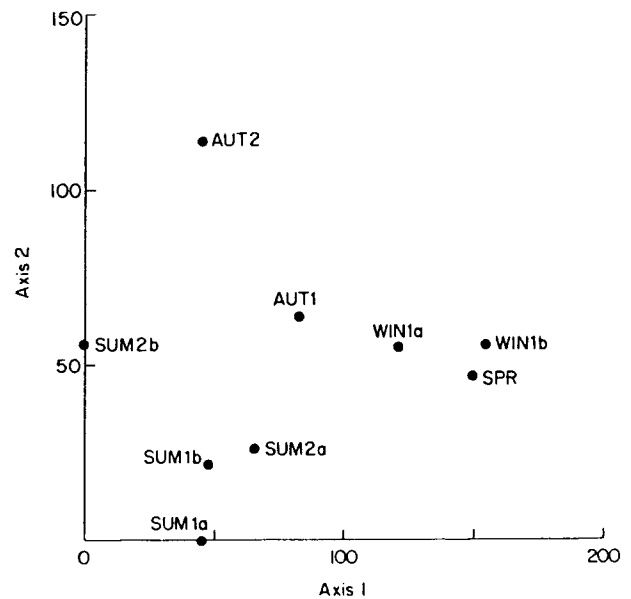


Fig. 2 Ordination diagram (DECORANA) of monthly drift samples. Total drift density for each month was standardized to 100 and individual species densities were adjusted accordingly. Rare taxa (see text) were excluded prior to ordination (acronyms as in Table 1).

Table 3 Seasonal changes in mean total drift density

a. Analysis of variance results (data was transformed with log(x+1), where x = Number of individuals per m³)

Source	Sum of squares	df	Mean square	F-ratio	P
Date	2.374	8	0.297	24.389	< 0.000
Error	0.122	10	0.012		

b. Ryan's test results (acronyms as in Table 1. Horizontal lines connect mean monthly drift densities, which were not significantly different from each other)

Time	AUT2	WIN1a	SUM2b	WIN1b	SPR	SUM2a	AUT1	SUM1a	SUM1b
Mean*	7.386	7.399	7.651	7.809	7.963	7.971	8.061	8.156	8.584

* Mean = log (number of individuals per m³ + 1).

Diel drift

Most of the forty-four taxa included in the analyses of diel drift had a constant drift pattern (Table 4). Fifteen taxa showed behavioural nocturnal drift (Table 4), in particular in the first summer, when total drift densities were highest (Fig.1, Table 4). However, behavioural drift was not restricted to a particular time of year, and all taxa showing behavioural drift did so in more than one season (Table 4). In only one month of the study (April 1983 = AUT2), was no behavioural drift recorded (Table 4). This coincided with a period of unusually low

discharge in the river and the lowest total drift densities (Fig.1).

Two species, *Zavreliella* sp.1 and 'Baetis' sp.MV2, showed neither a constant nor a behavioural drift pattern (Figs 3 and 4, Table 4). *Zavreliella* sp.1 was usually collected in high densities and drift densities which fluctuated with no consistent daily patterns (Fig. 3, Table 4). 'Baetis' sp.MV2, on the other hand, consistently drifted at high densities, but only over a short period of several hours around dawn and after dusk in summer (Fig. 4). Finch's test, as applied in this study, tested for changes in the level of drift between night and day, but

Table 4 Analysis of diel drift patterns. (a) Taxa showing constant drift (= increased nocturnal drift in no more than 1 month during the study). (b) Taxa showing behavioural drift (= increased nocturnal drift in more than 1 month during the study). (c) Taxa showing neither constant drift nor behavioural drift

	SUM1a	SUM1b	AUT1	WIN1a	WIN1b	SPR	SUM2a	SUM2b	AUT2
(a)									
Gastropoda spp.	-	-	0	0	-	0	-	-	0
Hydracarina spp.	0	0	-	0	0	0	0	0	0
<i>Riekoperla tuberculata</i> McLellan	0	-	-	0	-	0	0	-	-
<i>Dinotoperla serricauda</i> Kimmins	-	-	0	-	-	0	0	-	-
Tipulidae sp.1	0	-	0	0	-	0	-	-	-
<i>Chironomus</i> sp.1	-	-	-	0	0	-	-	-	-
<i>Paratanytarsus</i> spp.	0	0	-	-	-	0	0	0	-
<i>Rheotanytarsus</i> sp.	0	0	+	0	0	0	0	0	-
<i>Tanytarsus</i> sp.MV36E	0	0	+	0	0	0	0	0	0
<i>Calopsectra</i> sp.MV22E	-	0	0	-	0	-	0	-	0
<i>Polypedilum</i> spp.	-	-	0	0	-	-	-	-	-
<i>Macropelopia</i> sp.	-	0	0	0	0	+	-	-	-
<i>Pentaneura</i> sp.	0	-	-	-	-	-	0	-	-
<i>Podonomopsis</i> sp.1	0	-	0	0	0	+	0	-	-
<i>Podonomopsis</i> sp.2	-	0	0	0	0	0	-	-	-
Orthocladiinae sp.MV2E	0	-	-	-	0	0	0	-	-
Orthocladiinae sp.MV9E	0	0	-	0	0	0	0	-	-
Orthocladiinae sp.4	0	0	-	-	-	-	-	0	-
<i>Cricotopus</i> sp.MVB	0	0	-	-	-	-	0	0	-
Stratiomyidae sp.	-	-	-	-	0	-	-	-	0
<i>Ulmerochorema</i> sp.1	0	0	+	-	0	-	-	-	-
<i>Agapetus</i> spp.	0	-	0	0	0	0	0	-	0
Ecnomidae genus E sp.1	0	+	-	-	-	-	-	-	-
<i>Caenota plicata</i> Mosely	+	0	0	0	0	0	-	-	-
Philoreithridae spp.	-	0	0	0	-	-	0	-	-
Elmidae spp.	0	0	0	-	0	0	0	0	-
Helodidae spp.	-	0	0	0	+	0	-	-	0
(b)									
<i>Pseudomoera fontana</i>	+	+	+	0	0	0	0	0	0
<i>Illiesoperla australis</i> Tillyard	+	0	0	+	+	0	+	+	0
<i>Riekoperla williamsi</i>	+	-	0	0	+	+	+	-	-
<i>Dinotoperla eucumbene</i> McLellan	+	0	+	0	0	0	0	0	0
<i>Austrocercella mariannae</i> Illies	+	+	0	0	-	0	0	+	-
<i>Nousia</i> sp.A1	+	+	+	+	0	+	+	+	0
<i>Nousia</i> sp.A2	+	+	0	0	+	+	+	-	0
' <i>Baetis</i> ' sp.MV3	+	+	0	0	+	0	+	0	0
<i>Coloburiscoides</i> sp.1	+	+	0	+	+	+	+	0	0
<i>Austrosimulium mirabile</i>	+	+	0	+	0	0	+	+	0
<i>Austrosimulium furiosum</i> (Skuse)	+	+	0	0	0	+	0	0	0
<i>Hydrobiosella</i> spp.	+	+	+	0	+	0	+	+	0
Hydropsychidae genus M sp.1	+	+	+	0	+	+	+	+	0
<i>Alloecella grisea</i>	+	+	0	+	0	0	+	0	0
<i>Condocerus paludosus</i>	+	+	+	+	+	+	+	0	0
(c)									
<i>Zavreliella</i> sp.	0	0	0	0	0	0	0	0	0
' <i>Baetis</i> ' sp.MV2	0	0	0	0	0	0	0	0	0

+ = increased level of nocturnal drift with $L(A)_{\text{dusk}}$ and $L(A)_{\text{dawn}} < 0.05$, 0 = no change in the level of drift, both at dusk and at dawn (i.e. $L(A)_{\text{dusk}}$ and/or $L(A)_{\text{dawn}} > 0.05$). $L(A)_{\text{dusk}}$ = the probability, calculated from Finch's test, that the level of drift increased after dusk, and $L(A)_{\text{dawn}}$ = the probability that the level of drift decreased after dawn; - = taxon was absent or rare.

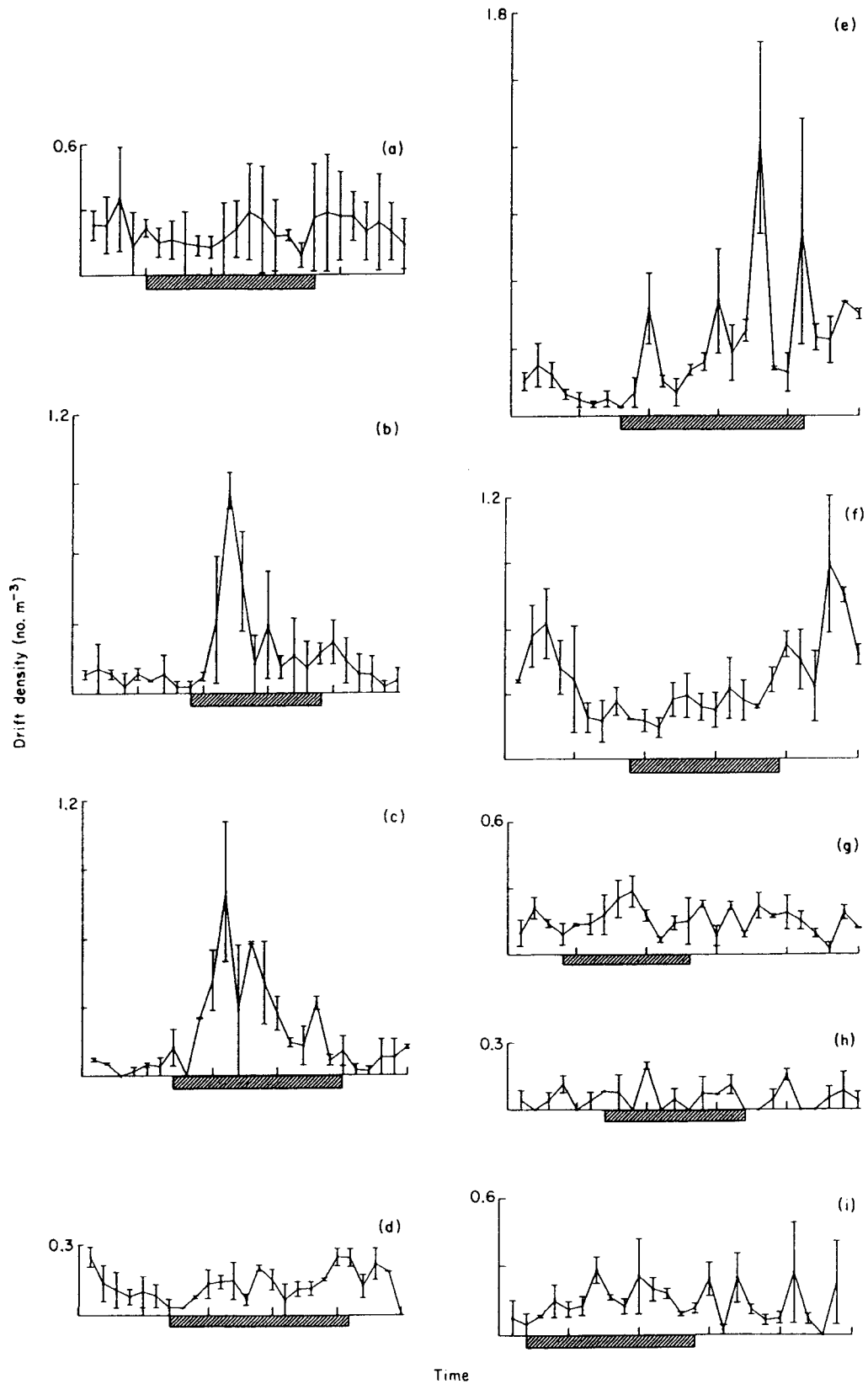


Fig. 3 Diel drift patterns of *Zavreliella* sp.1 in different seasons. (a) = SUM1a, (b) = SUM1b, (c) = AUT1, (d) = WIN1a, (e) = WIN1b, (f) = SPR, (g) = SUM2a, (h) = SUM2b and (i) = AUT2 (symbols as in Table 1). The shaded bars on the x-axes represent night-time. Error bars represent the range of drift densities sampled by the nets.

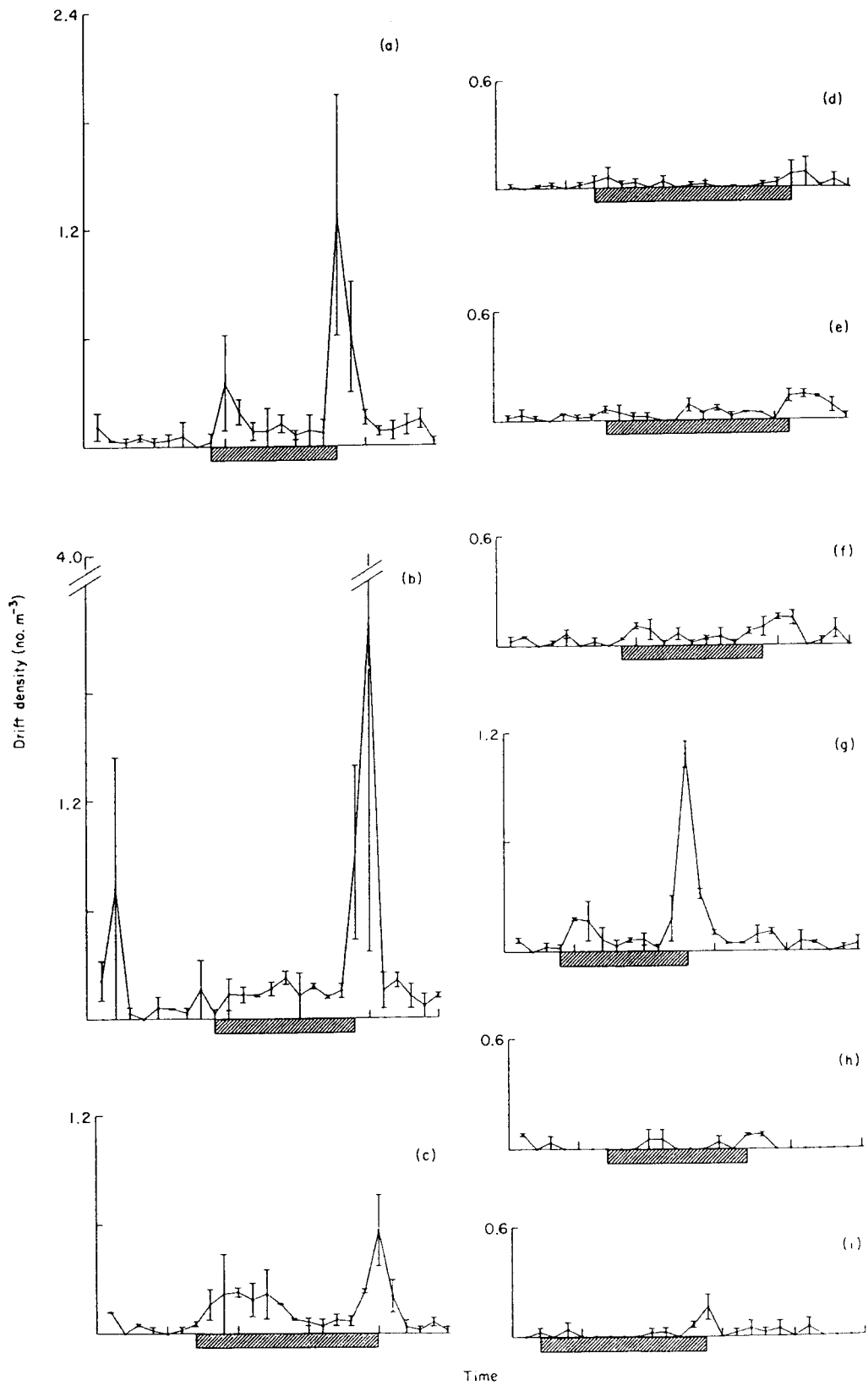


Fig. 4 Diel drift patterns of *Baetis* sp. MV2 in different seasons, (a) = SUM1a, (b) = SUM1b, (c) = AUT1, (d) = WIN1a, (e) = WIN1b, (f) = SPR, (g) = SUM2a, (h) = SUM2b and (i) = AUT2 (symbols as in Table 1). The shaded bars on the x-axes represent night-time. Error bars represent the range of drift densities sampled by the nets.

did not allow for the detection of short-term, crepuscular peaks. *Baetis* sp. MV2 did not sustain high drift density throughout the night (Table 4), and thus was not classified as showing nocturnal behavioural drift.

Discussion

The drift of benthic invertebrates is a universal phenomenon with members of many benthic taxa participating (Brittain & Eikeland, 1988). Total drift represents a mosaic of drift densities of different species, which depends on the species present in the benthos, and on their propensity to drift. In this study only a few of the taxa collected contributed to a large part of total drift density. Whether this reflects the relative abundances of these taxa in the benthos, or their high propensity to drift, cannot be determined without specifically examining the relationship between drift and benthos of the taxa involved. In a density-dependent relationship between drift and benthos, the former will reflect the abundance and composition of the latter (Dimond, 1967; Wiley, 1981; Allan, 1987). However, many instances of density-independent relationships between drift and benthos have also been documented (Dudgeon, 1983; Krueger & Cook, 1984; Benson & Pearson, 1987; Statzner, Elouard & Dejoux, 1987).

Drift varied with season, with peaks of total drift in summer and spring. This reflected the drift of most of the common taxa. A summer peak in total drift has also been described for temperate streams elsewhere (Clifford, 1972; Bishop and Tilzey, 1978; Hemsworth & Brooker, 1981; Sandlund, 1982; Obi & Connor, 1986). On the other hand, in other temperate streams drift was highest in spring and autumn, with low drift in summer (Armitage, 1977; Stoneburner & Smock, 1979; Angermeier, 1982; Day, Anderson & Grubaugh, 1992). This discrepancy in pattern could be associated with differences in species composition between studies, as well as changes in drift during the life cycle of single species (Brittain & Eikeland, 1988). For example, *Dinotoperla eucumbene* showed little drift in winter, a period which could have coincided with low recruitment and low benthic densities of this species (Yule, 1985). However, as little information exists on the life histories of stream insects in temperate Australian streams (Marchant, 1986), further interpretation of drift patterns in relation to life histories is not possible here.

Most seasonal studies of drift examine changes in total drift densities or describe taxon-specific patterns

(Armitage, 1977; Krueger & Cook, 1984; Obi & Connor, 1986; Allan, 1987; Benson & Pearson, 1987; Dudgeon, 1990). It was found that the seasonal pattern in total drift density reflected that of the common taxa. However, using ordination analysis it was possible to decrease the influence of abundant taxa, and examine seasonal patterns in drift composition. Drift samples collected in both summers were found to be more similar to each other in composition than to samples taken at other times of year. This pattern differed from that of total drift, where the differences in densities between summers was as great as the difference between winter drift density and that of the second summer. Thus ordination provided a means of detecting a seasonal pattern, which was based on taxonomic composition and abundances of all drifting taxa, instead of just on the most abundant taxa.

Stream discharge is one of the major abiotic factors influencing drift densities (Brittain & Eikeland, 1988). Both increases and decreases in discharge can result in high drift densities associated with catastrophic drift (Corarrino & Brusven, 1983; Perry & Perry, 1986; Rae, 1987). No evidence was found of catastrophic drift on the dates that I sampled, during a period of low discharge associated with a drought. On the contrary, many taxa showed decreased drift during this period. However, different drift responses may be elicited by the abrupt change of flow associated with an experimental reduction of discharge (Minshall & Winger, 1968) or the closure of a dam (Blyth, Doeg & StClair, 1984), than by the relatively more gradual reduction in discharge caused by a drought. It is necessary to understand the mechanism by which decreases in flow can increase drift before these differing observations can be interpreted.

Predation has been identified as a possible source of selection pressure in the evolution of nocturnal behavioural drift (Allan, 1978; Flecker, 1992), a condition which has been documented for many benthic taxa. Unfortunately, the criteria for deciding whether a species is showing nocturnal behavioural drift are often not clearly defined. For example, a species is usually considered to show nocturnal drift if peaks in drift density occur at night (Waters, 1972). Peaks, however, are often identified on the basis of insufficient replication (see Allan & Russek, 1985) during one particular time period, such as 1 h, relative to the next. In this study a new technique in the analysis of drift has been used, time series analysis, to provide a consistent criterion for

deciding when the level of drift of a particular taxon is higher at night than during the day. It was found that one particular taxon of Ephemeroptera, '*Baetis*' sp.MV2, showed peaks in drift during a short time period relative to the next, but did not drift at higher densities overall during the night than during the day. Thus, avoidance of predation during the day alone can not explain the drift pattern of this taxon.

Several categories of drift have been described in the literature (Waters, 1972). This has been useful in that it recognizes the multifaceted nature of drift. However, it can also lead to the expectation that the drift of all invertebrates conform to one of these categories. This was not the case in this study, with one of the most abundant taxa in the drift, *Zavreliella* sp.1, showing a very erratic pattern with increases in drift density occurring unpredictably throughout a 25-h period at different times during the year. This did not fit into previously identified categories of drift, but it is considered that the establishment of further categories would not be particularly useful and would only lead to confusion (Brittain & Eikeland, 1988).

In conclusion, whilst drift has been documented as a common phenomenon in streams, it represents a conglomerate of many activities of different invertebrate taxa. As such, it is influenced by many different factors, of both an abiotic and biotic nature, and may be of different ecological significance in different systems. Thus it may be more appropriate to study drift within the context of a particular ecological question, such as the colonization of denuded substrates or avoidance of predation, than as a phenomenon in its own right. In addition, many studies have not been very rigorous in the collection and analysis of drift samples and provide a poor basis for future work. The execution of drift sampling may be relatively easy, but the design of useful studies involving drift is not.

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Appendix 1 Seasonal patterns in drift: ANOVA and Ryan's test results for mean monthly drift densities of the nineteen most common taxa. For all ANOVA tests: harmonic mean $n = 2.41$; all data $\log(x+1)$ transformed unless otherwise indicated, where $x =$ number of individuals per m^3 ; $F = F$ -ratio; *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$; df = error degrees of freedom. Horizontal lines connect mean monthly drift densities that were not significantly different from each other as determined by Ryan's test

<i>Pseudonoeira fontana</i>									
AUT2	WIN1a	SUM2b	WIN1b	SPR	AUT1	SUM2a	SUM1b	SUM1a	
2.507	3.327	3.543	3.818	4.050	4.479	4.959	5.648	5.650	
				df = 10	$MS_E = 0.024$	F = 103.409***			
<i>Illiesoperla australis</i>									
AUT2	SUM1b	WIN1a	WIN1b	SUM2b	AUT1	SPR	SUM2a	SUM1a	
2.302	3.044	3.116	3.203	3.232	3.456	3.533	4.143	4.216	
				df = 10	$MS_E = 0.158$	F = 4.817*			
<i>Dinotoperla eucumbene</i>									
WIN1a	WIN1b	AUT2	SPR	SUM2b	AUT1	SUM1b	SUM2a	SUM1a	
1.757	2.456	2.996	3.272	3.350	3.445	3.994	4.108	4.248	
				df = 10	$MS_E = 0.196$	F = 7.244**			
<i>Riekoperla williamsi</i>									
SUM1b	AUT2	SUM2b	AUT1	SUM1a	SUM2a	WIN1a	WIN1b	SPR	
0.000	0.000	0.647	2.776	3.278	3.441	4.417	5.433	5.479	
				df = 10	$MS_E = 0.156$	F = 60.647***			
<i>Austrocercella mariannae</i> (data not transformed)									
WIN1b	WIN1a	AUT2	AUT1	SUM2b	SPR	SUM2a	SUM1b	SUM1a	
5.185	5.590	6.000	10.360	11.655	11.750	47.215	119.48	131.760	
				df = 10	$MS_E = 26.652$	F = 233.599***			
<i>Nousia</i> sp.A1									
SUM2b	AUT2	WIN1b	SUM2a	WIN1a	SPR	SUM1a	AUT1	(SUM1b)†	
3.215	4.072	4.436	4.530	4.598	4.609	4.907	5.281	(6.008)†	
				df = 9	$MS_E = 0.014$	F = 55.703***			
'Baetis' sp.MV2									
SUM2b	AUT2	WIN1b	SPR	WIN1a	SUM2a	AUT1	SUM1a	(SUM1b)†	
2.723	3.116	3.793	3.882	3.945	4.736	4.769	5.048	(5.334)†	
				df = 9	$MS_E = 0.035$	F = 42.859***			
'Baetis' sp.MV3									
SPR	AUT1	WIN1b	WIN1a	AUT2	SUM2b	SUM2a	SUM1a	SUM1b	
2.994	3.141	3.206	3.236	3.367	3.664	4.301	5.268	5.298	
				df = 10	$MS_E = 0.085$	F = 22.271***			
<i>Austrosimulium furiosum</i> (data not transformed)									
AUT2	AUT1	SUM2b	WIN1a	WIN1b	SPR	SUM1b	SUM2a	SUM1a	
4.535	9.905	19.170	20.770	24.665	28.335	35.130	51.075	60.070	
				df = 10	$MS_E = 83.833$	F = 9.282**			

Appendix 1 (cont'd)

<i>Austrosimulium mirabile</i>				df = 10	$MS_E = 0.061$	$F = 32.589^{***}$		
WIN1b	WIN1a	SPR	AUT1	SUM2a	AUT2	SUM2b	SUM1a	SUM1b
3.457	3.678	4.021	4.965	5.117	5.470	5.749	5.834	5.989
<i>Rheotanytarsus</i> sp. (data not transformed)				df = 10	$MS_E = 123.918$	$F = 20.856^{***}$		
AUT2	WIN1a	WIN1b	SPR	AUT1	SUM2a	SUM1a	SUM2b	SUM1b
6.185	16.680	20.475	33.020	33.345	46.780	51.843	98.535	110.065
<i>Podonomopsis</i> sp. (data not transformed)				df = 10	$MS_E = 125.701$	$F = 41.334^{***}$		
AUT2	SUM1b	SUM2b	AUT1	WIN1a	SUM1a	SUM2a	WIN1b	SPR
0.885	2.525	2.870	8.625	11.790	48.803	70.035	92.270	144.960
<i>Thienemaniella</i> sp.MV10E				df = 10	$MS_E = 0.122$	$F = 14.753^{***}$		
SPR	WIN1b	WIN1a	AUT1	SUM1a	AUT2	SUM2a	SUM1b	SUM2b
1.810	2.138	2.171	2.624	3.042	3.626	4.087	4.147	4.192
<i>Zavreliella</i> sp.1				df = 10	$MS_E = 0.147$	$F = 4.610^*$		
SUM2b	WIN1a	AUT2	SUM1b	SUM2a	AUT1	SUM1a	WIN1b	SPR
3.860	4.831	4.909	4.993	5.048	5.188	5.235	5.704	5.906
<i>Tanytarsus</i> sp.MV36E				df = 10	$MS_E = 0.104$	$F = 13.883^{***}$		
SUM2a	SUM2b	WIN1a	AUT2	SUM1a	AUT1	SPR	WIN1b	SUM1b
2.935	3.310	3.597	3.632	3.849	4.231	4.484	4.814	5.706
<i>Hydrobiosella</i> sp.				df = 10	$MS_E = 0.049$	$F = 12.354^{***}$		
SPR	WIN1a	WIN1b	AUT1	SUM2b	SUM1b	AUT2	SUM1a	SUM2a
3.163	3.495	3.717	3.959	3.972	4.251	4.293	4.372	5.011
<i>Agapetus</i> spp.				df = 10	$MS_E = 0.094$	$F = 15.246^{***}$		
SUM1b	SUM2b	AUT2	AUT1	WIN1a	WIN1b	SUM1a	SUM2a	SPR
2.065	2.218	2.926	2.999	3.179	3.595	4.095	4.223	4.243
<i>Alloecella grisea</i>				df = 10	$MS_E = 0.045$	$F = 13.197^{***}$		
SUM2b	AUT2	SUM1b	SUM1a	SUM2a	SPR	WIN1a	WIN1b	AUT1
3.109	3.534	4.074	4.104	4.276	4.472	4.648	4.672	4.675
<i>Condocerus paludosus</i>				df = 10	$MS_E = 0.084$	$F = 13.747^{***}$		
SUM1a	SUM2b	WIN1a	SUM2a	AUT2	WIN1b	SPR	SUM1b	AUT1
3.311	3.801	4.041	4.094	4.180	4.571	4.643	5.291	5.568

† = outlier, not included in the analysis.