J. N. Am. Benthol. Soc., 1995, 14(1):147-157

Gene flow among conspecific populations of *Baetis* sp. (Ephemeroptera): adult flight and larval drift

SONJA K. SCHMIDT, JANE M. HUGHES, AND STUART E. BUNN

Faculty of Environmental Sciences, Griffith University, Nathan, Queensland 4111 Australia

Abstract. The genetic structure of populations of *Baetis* sp. (Ephemeroptera:Baetidae) was used to draw inferences about the means of dispersal within and between stream systems of the Conondale Range, Queensland, Australia. Allozyme electrophoresis was used to examine allelic frequencies at five variable loci in geographically distant populations of nymphs in the same drainage and in nearby populations in different drainages.

The results showed widespread gene flow between drainages and a tendency for local differentiation. We concluded that adult flight represents an effective means for dispersal between drainage systems. The differentiation between populations at a local scale and erratic deviations from Hardy Weinberg equilibrium could have occurred if the nymphs collected from any stream were the offspring of only a few adults. If this is the case, the dispersal capabilities of nymphs by swimming, crawling or drift may be minimal even within a single stream.

Key words: dispersal, gene flow, drift, stream insects, *Baetis*, rainforest streams, allozyme electrophoresis.

Stream insects can potentially disperse as stream-living larvae or as aerial adults. Methods of stream dispersal include crawling, swimming, and larval drift (Mackay 1992). Swimming and crawling are generally thought to operate on a small spatial scale, and it is widely accepted that larval drift and adult flight are the principal mechanisms by which stream insects disperse over a wide area (Hynes 1970, Williams and Hynes 1976, Minshall and Petersen 1985). However, the significance of adult flight and larval drift and, more particularly, their relative importance as a means for dispersal are not completely understood.

In comparison with terrestrial species, the adults of stream insects are typically short-lived and many have limited powers of flight (Hynes 1970). Although flight is accepted to have a major role in the dispersal of terrestrial insects, its role as a mechanism for the dispersal of aquatic insects may not be as significant (Hynes 1970). Müller (1954, 1982) maintained that larval drift represents the primary mechanism for colonising new areas. Others have argued that the larvae present in drift may be less fit than nondrifters and incapable of effective dispersal (Waters 1961, 1972, Minshall and Petersen 1985).

The significance of adult flight or larval drift as mechanisms of dispersal is difficult to establish because few studies have provided estimates of the extent of successful dispersal due to either mechanism. Further, the relative importance of adult flight and larval drift is likely to be taxon specific, being dependent on adult life span and the swimming capability of larvae. Hence we need to derive reliable estimates of the extent of both larval and adult dispersal for a variety of species.

The extent of dispersal of stream invertebrates can be estimated directly or indirectly. Direct methods have included the marking of individuals (Erman 1986) and the use of ^{32}P analysis (Hynes 1970). A disadvantage of such methods is that, despite its potential significance, long-distance movement may be too rare to be measured directly (Slatkin 1985). To overcome the problems associated with the restricted time scale available for direct observation, a widely used indirect method is to investigate the genetic structure of populations by using the spatial distribution of alleles at protein loci detected by allozyme electrophoresis (Slatkin 1985). The advantage of this technique is that the observed patterns reflect the evolutionary history of populations. Allozyme electrophoresis is gaining popularity with stream ecologists; however, to date, few studies have investigated the genetic structure of populations of aquatic insects. Recent studies have examined stream populations of waterstriders (Zera 1981, Preziosi and Fairbairn 1992), black flies (Snyder and Linton 1984), mayflies (Sweeney et al. 1986, 1987), and caddisflies (Jackson and Resh 1992).

The genetic structure of natural populations

results largely from the action of three evolutionary forces: gene flow, genetic drift, and natural selection (Allendorf and Phelps 1981). Since gene flow is a collective term that includes all mechanisms resulting in the movement of genes from one population to another, gene flow can be used as a measure of dispersal (Slatkin 1985). The genetic structure of conspecific populations from two different localities will be similar if the populations have been connected by substantial gene flow. If gene flow is limited, then random genetic drift is likely to cause differences in the genetic structure of these populations. This interpretation, however, depends on the action of natural selection (Slatkin 1987).

Selective neutrality is usually assumed when interpreting patterns of genetic differentiation (Allendorf and Phelps 1981). A comparison of the patterns of differentiation at different loci may suggest this assumption is not valid. Patterns of genetic differentiation between local populations maintained by genetic drift and gene flow will tend to be similar across all loci (Cavalli-Sforza 1966). On the other hand, the action of natural selection could cause differences in the patterns observed among loci (Slatkin 1987).

Our study aimed to analyse the genetic structure of conspecific populations and to use this to infer the relative importance of adult flight and larval drift as mechanisms for dispersal for a common species of *Baetis* (Ephemeroptera:Baetidae) found in rainforest streams of the Conondale Range in southeast Queensland. We predicted that, if adult flight represents the more important means for dispersal, and if there are no barriers to adult dispersal in different drainages other than distance, little genetic divergence is expected between nearby populations in different drainages. Conversely, if larval drift represents the more important mechanism of dispersal, geographically distant populations within the same drainage, between which larval drift may result in gene flow, will be more genetically similar than nearby populations in different drainages, where larval drift can be discounted as a means of genetic exchange.

The adult stages of Ephemeroptera typically have a short life span, usually between one and three days, and do not feed (Sweeney et al. 1986). *Baetis* nymphs are agile swimmers and are considered to be rapid recolonisers of disturbed areas (Mackay 1992). With these characteristics, it might be expected that *Baetis* would disperse more widely within a drainage system than between drainages.

Study Sites

The Conondale Range lies between Kilcoy and Kenilworth, Queensland (Fig. 1). The range separates stream systems that drain into the Brisbane River from those draining into the Mary River. The climate of the region is subtropical with hot wet summers and mild dry winters. The annual rainfall is approximately 1500 mm (Australian Bureau of Meteorology 1983).

Throughout this paper the following terms are used:

"Subcatchments" consist of two neighbouring streams.
"Drainages" consist of two subcatchments within the same drainage system.
"Areas" consist of two subcatchments each within different drainage systems.

Four small subcatchments, two on either side of the range, were selected. The Booloumba and Upper Mary subcatchments drain into the Mary River, and the Stony and Kilcoy subcatchments drain into the Brisbane River. We have named the areas "Eastern" and "Western". The western area includes the Booloumba and Kilcoy subcatchments and the eastern area includes the Stony and Upper Mary subcatchments (Fig. 1). The western area is more northerly than the eastern area. The location of the subcatchments is such that those in different drainages are geographically closer to each other than to those within the same drainage system. For example, streams within the Upper Mary subcatchment in the Mary drainage are separated from those in the Stony subcatchment in the Brisbane drainage by several hundred metres. In contrast, streams within the Upper Mary subcatchment and those in the Booloumba subcatchment, also in the Mary drainage, are separated by approximately 10 km of forest and 30 km of stream channel.

There is little possibility of aquatic dispersal between the two drainage systems. The Mary River flows into the sea at Maryborough, about 220 km north of the mouth of the Brisbane Riv-

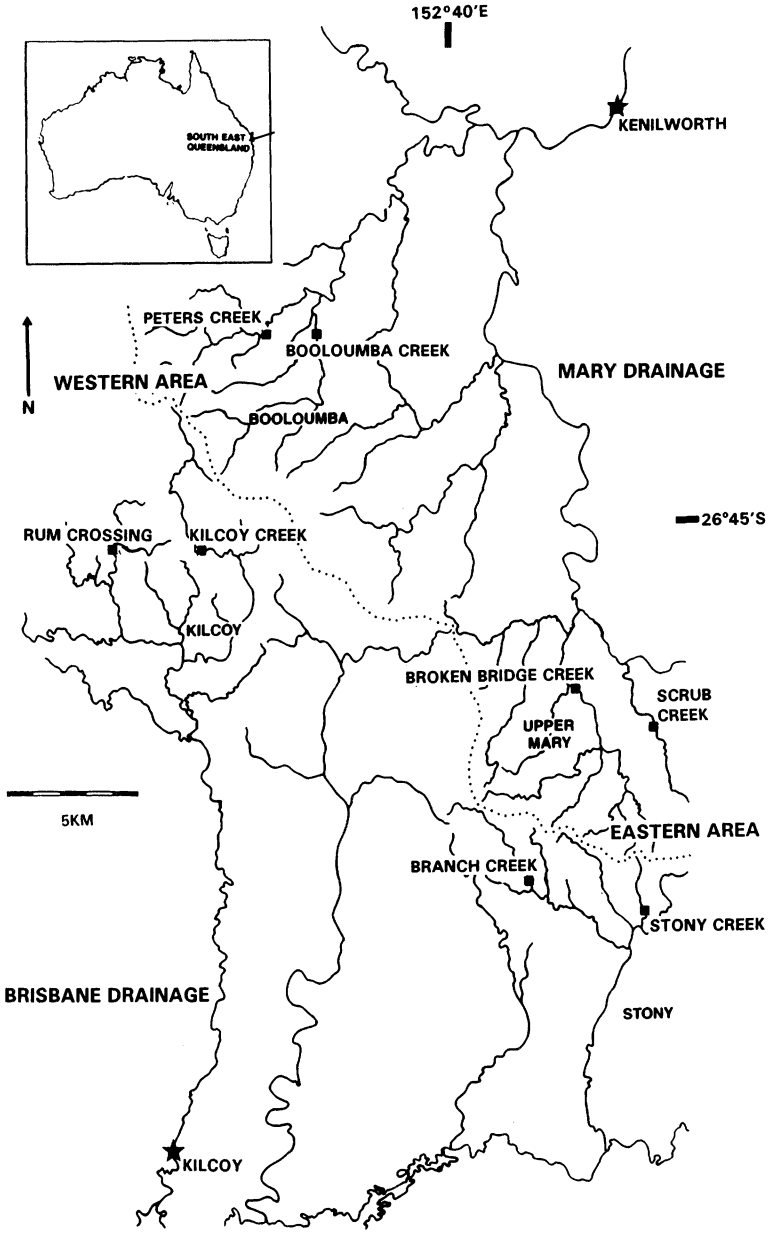

FIG. 1. Study sites on streams in the Mary River and Brisbane River drainages. Note that headwater streams within a particular Area (Eastern or Western) are geographically closer to those in the opposite drainage than they are to those in the same drainage but a different Area. The dotted line shows the Conondale Range. Inset map shows the general location of the drainages in southeast Queensland.

er; thus headwater streams in the two drainages are separated by a total aquatic distance of over 700 km.

Sampling was largely conducted in areas of State Forest. Sampling sites in the Stony, Kilcoy, and Booloumba subcatchments were situated in subtropical rainforest and wet sclerophyll forest. Sites in the Upper Mary subcatchment were

bordered by private farms where the surrounding vegetation had been cleared. A more detailed description of the study area can be found in Hughes et al. (1995).

Methods

Collection

Sampling was conducted between 26 March 1992 and 27 April 1992. Late instar *Baetis* sp. nymphs, recognised by the presence of darkened wing pads, were collected by sweeping a hand net along the surface of rocks. The species was chosen because it is common and widespread throughout the area. Collections were confined to a few pools at each site, usually 10–40 m (and a maximum of 100 m) of stream. Nymphs were preserved in liquid nitrogen and, on return to the laboratory, samples were stored at −70°C for later treatment.

Two streams were sampled within each subcatchment: Stony Creek and Branch Creek within the Stony subcatchment, Booloumba Creek and Peters Creek within the Booloumba subcatchment, Kilcoy Creek and Rum Crossing within the Kilcoy subcatchment, and Scrub Creek and Broken Bridge Creek within the Upper Mary subcatchment (Fig. 1).

Electrophoresis

We conducted cellulose acetate electrophoresis. Fourteen enzymes were initially screened for their suitability. PEPC, PGD, and MDH appeared monomorphic (i.e., the frequency of the most common allele was greater than 0.95), while PGI, PGM, MPI, AMY, IDH, BEST, ESTD, and PEPB were polymorphic. PEPA, GOT, and ADH were not decipherable with the initial running conditions used. Five polymorphic loci were chosen for their ease of interpretation: *PepB, Mpi, Pgi, Amy* and *Pgm*. The running conditions and enzyme staining overlays are adapted from Hebert and Beaton (1989). All presumed allelic homologies between sites were verified by testing a representative from each population on the same gel.

Analysis

F_{is} values (Wright 1978) were calculated for each stream population to compare genotypic frequencies observed with those expected under Hardy-Weinberg equilibrium.

A hierarchical analysis of genetic differentiation was used to examine the genetic structure of conspecific populations. The sampling design represents two separate spatial hierarchies; streams within subcatchments within drainages, and streams within subcatchments within areas. To analyse the extent of differentiation among subpopulations, hierarchical F statistics (F_{st}) (Wright 1965, 1978, Nei 1977) were calculated using BIOSYS version 1.6 (Swofford and Selander 1981). The approach taken resembles that used by Rank (1992), in that F statistics were calculated separately for each level in the spatial hierarchies described above. This approach was taken because the individual measurements show more clearly how the patterns of differentiation vary between streams within different subcatchments and how different subcatchments vary within drainages and areas.

The following F_{st} values were calculated. Subscripts define the populations used to calculate F_{st}.

F_{ss} represents the differentiation between streams within a given subcatchment.
F_{sd} represents the differentiation between subcatchments within a given drainage.
F_{sa} represents the differentiation between subcatchments within a given area.
F_{dt} represents the differentiation between drainages.
F_{at} represents the differentiation between areas.

Chi-squared tests were used to determine the statistical significance of the F_{st} and F_{is} values using the formulae given by Waples (1987). The relative magnitude of F_{st} values within and between the hierarchies was compared to determine the patterns of genetic differentiation and the extent of adult versus larval dispersal.

The interpretation of allelic frequencies requires that the sample consists of only a single species. A significant deviation from Hardy-Weinberg equilibrium or the presence of linkage disequilibrium between pairs of loci may show whether more than one species is present (Hartl and Clark 1989). In addition to the calculation of F_{is} values, all possible comparisons between the genotypes at pairs of loci were examined for each site, and the existence of linkage disequilibrium was tested using a Chi-squared test of independence.

TABLE 1. The fixation index (F_{is}) within each population sampled at each of five polymorphic loci.

Site	Locus				
	PepB	*Mpi*	*Pgi*	*Amy*	*Pgm*
Branch Creek	−0.057	0.228**	−0.018	0.104	0.293***
Stony Creek	0.027	0.144	−0.099	0.227	0.405***
Scrub Creek	0.111	0.161	0.135	0.574***	0.110
Broken Bridge Creek	0.088	0.257**	0.309***	0.127	0.095
Peters Creek	0.115	−0.073	0.276***	0.077	0.074
Booloumba Creek	0.134	0.162	0.113	0.258*	0.243***
Rum Crossing	0.137	0.100	0.000	−0.065	0.105
Kilcoy Creek	−0.031	0.030	0.185	0.096	0.053

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Results

The loci that were polymorphic in the original screening were polymorphic in each stream (Appendix 1). In general, the most common allele at a particular locus was most common across all sites. For this reason the F_{st} values obtained between populations were reasonably small.

Deviations from Hardy-Weinberg equilibrium

Genotypic frequencies in populations at Rum Crossing and Kilcoy Creek were found to be in Hardy-Weinberg equilibrium at all of the loci studied ($p > 0.05$) (Table 1). However, genotypic frequencies at all loci apart from *PepB* deviated significantly from those expected under Hardy-Weinberg equilibrium at at least one of the other sites. The observed deviations are highly significant and no consistent pattern was apparent at any locus or site. However, the positive F_{is} values show that a deficiency in heterozygotes was responsible for the observed deviations from Hardy-Weinberg equilibrium. In most cases, a deficiency of the most common heterozygote contributed to these deviations.

Of the eighty pairwise comparisons conducted to determine the presence of linkage disequilibrium at each site, only one was significant ($p < 0.05$), a result that could be expected by chance.

Genetic differentiation between conspecific populations

The F_{dt} values for individual loci provide contrasting estimates of the degree of genetic differentiation between drainages. There was no significant differentiation between the Mary and Brisbane drainages at the *PepB*, *Mpi*, or *Amy* loci ($p > 0.05$). However, drainages differed significantly at the *Pgi* and *Pgm* loci ($p < 0.05$), although the values themselves were very similar in magnitude to those observed at the other loci (Table 2).

Individual loci exhibited different patterns of differentiation among areas. In this case, however, some loci exhibited strong differentiation and others showed little or no differentiation. F_{at} values for *PepB* and *Amy* reflected significant genetic differentiation between areas ($p < 0.001$). In contrast, allele frequencies were homogeneous at *Mpi*, and *Pgi* ($p > 0.05$). The F_{at} at *Pgm*, though significant ($p < 0.01$), was an order of magnitude less than that for *PepB* and *Amy* (Table 3).

By examining the patterns of differentiation between subcatchments, it can be seen that the heterogeneity in allele frequencies found at the *Pgm* locus between drainages can be attributed

TABLE 2. F_{st} values for the subcatchments within the western and eastern areas and among drainages.

F-statistic	Locus				
	PepB	*Mpi*	*Pgi*	*Amy*	*Pgm*
F_{sa} (western)[a]	0.001	0.004	0.005*	0.002	0.002
F_{sa} (eastern)[b]	0.003	0.001	0.002	0.006	0.021***
F_{dt}[c]	0.001	0.002	0.003*	0.001	0.003*

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

[a] Differentiation between drainages in the western area.

[b] Differentiation between drainages in the eastern area.

[c] Differentiation between drainages.

TABLE 3. F_{st} values for the Brisbane and Mary river drainages and among areas.

	Locus				
F-statistic	*PepB*	*Mpi*	*Pgi*	*Amy*	*Pgm*
F_{sd} (Brisbane)[a]	0.009**	0.001	0.001	0.039***	0.015***
F_{sd} (Mary)[b]	0.021***	0.000	0.000	0.007*	0.004
F_{at}[c]	0.016***	0.000	0.000	0.019***	0.002

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.
[a] Differentiation between areas in the Brisbane drainage.
[b] Differentiation between areas in the Mary drainage.
[c] Differentiation between areas.

to differences between subcatchments on opposite sides of the range in the east area. Similarly, the differentiation found between drainages at the *Pgi* locus can be attributed to differences between subcatchments within the west area (Table 2). Further, in some cases, the differentiation between areas can be attributed to differentiation between subcatchments within drainages. At *Pgm* and *Amy* loci, the differentiation between areas can be attributed to differences between subcatchments in the Brisbane drainage (Table 3).

Significant differentiation between streams within subcatchments was also found (Table 4). The magnitude of the F_{st} values in these cases indicate that the genetic differentiation between populations at a smaller spatial scale is, in some cases, equivalent to or greater than that found between populations at a larger scale.

Discussion

Genetic differentiation between conspecific populations

We predicted that, if adult dispersal was the primary mechanism of dispersal for aquatic insects, then neighbouring streams in different drainage basins would be more genetically similar than distant streams in the same drainage. Conversely, if larval drift and other mechanisms of stream dispersal represent the most effective means to disperse, streams within the same drainage system would be expected to be more similar than those in different drainage basins. The data do not fit either of these patterns consistently. Different patterns of differentiation between drainages and areas were observed at different loci. However, the lack of marked differentiation between populations at any level of the spatial hierarchies described, the comparatively low levels of differentiation between drainages observed at the *Pgi, Pgm, PepB,* and *Amy* loci, and the homogeneity in allele frequencies recorded at the *Mpi* locus suggest there is widespread aerial dispersal at least between drainages.

What is most interesting about the observed patterns of genetic differentiation is that the differentiation found on a large spatial scale can be attributed to the differentiation at a smaller spatial scale. In some cases, the differentiation between populations within a single subcatchment was an order of magnitude greater than that observed between populations inhabiting different areas or drainages. This tendency for greater differentiation between populations at a small scale cannot be explained by the move-

TABLE 4. F_{ss} values between streams in a subcatchment for each locus.

	Locus				
Subcatchment	*PepB*	*Mpi*	*Pgi*	*Amy*	*Pgm*
Stony	0.012*	0.004	0.002	0.006	0.003
Upper Mary	0.003	0.000	0.008	0.027***	0.018**
Booloumba	0.004	0.002	0.001	0.002	0.009*
Kilcoy	0.002	0.005	0.012*	0.013*	0.002

*** $p < 0.005$, ** $p < 0.01$, * $p < 0.05$.

ment between sites. If allele frequencies are homogeneous between populations on a large scale then, over this distance, gene flow is sufficient to overcome the disruptive effects of genetic drift. If gene flow is sufficient over the largest distances, sites closer together should also be connected by gene flow. We suggest that this pattern of genetic differentiation and erratic deviations from Hardy-Weinberg equilibrium are related.

Deviations from Hardy-Weinberg Equilibrium

Many studies of the genetic structure of natural populations have reported a significant deficiency in heterozygotes (Zouros and Foltz 1984, Crouau-Roy 1988), including studies of species of aquatic insects (Robinson et al. 1992, Sweeney et al. 1987, Snyder and Linton 1984). Because of the inconsistencies among sites and across loci we believe that none of the commonly invoked hypotheses adequately explain the patterns found in our study.

Of most concern was the possibility that more than one species was examined. However, if more than one species was present, all loci would be expected to exhibit a similar pattern of heterozygote deficiency. Inbreeding, or the sampling of a number of discrete subpopulations, is also expected to affect all loci in a similar manner (Richardson 1982, Crouau-Roy 1988, Sweeney et al. 1987). Finally, the lack of linkage disequilibrium suggests that the samples taken at each site consisted of only a single species.

It is unlikely that problems in the interpretation of gels for a particular locus would occur at only some sites. In any case, the enzyme systems examined resolved well under the conditions used. Similarly, inconsistency across sites would not be expected if natural selection against heterozygotes was responsible for the deficiencies observed unless conditions amongst streams varied considerably. Furthermore, the tendency for the deficiency of heterozygotes to be found at many classes of heterozygotes would suggest that, for selection to be responsible for the patterns observed, severe disruptive selection would be required and this is considered extremely unlikely (Richardson 1982).

Null or silent alleles do not give any band on the electrophoretic plate and consequently, when we stained for a monomer, a heterozygote for a null allele would be scored as an active homozygote and result in an apparent heterozygote deficiency. In general, null alleles are considered rare in natural populations and appear to be associated with esterases (Zouros and Krimbas 1969). If null alleles were present in sufficient frequencies to cause the marked deficiencies recorded, null homozygotes should have been observed. Null homozygotes produce no band. The only locus where individuals commonly did not resolve was *Amy*. Null alleles may segregate at this locus at some sites and may have caused the deficiencies in heterozygotes observed at this locus but are unlikely to explain the deviations found at the other loci.

Among the assumptions of the Hardy-Weinberg principle is that the population sampled is very large (Hartl and Clark 1989). Although *Baetis* sp. nymphs were abundant in all streams, such abundance might be illusory since most aquatic insect species are fecund and typically produce clutches in the range of 200–2000 eggs (Wilzbach and Cummins 1989). For example, *Baetis rhodani* lays up to 4500 eggs per female (Elliott and Humpesch 1980). Wilzbach and Cummins (1989) suggested that oviposition by only a few adult females could populate an entire section of stream. Therefore, it is possible that the *Baetis* sp. nymphs sampled may represent the offspring of a small number of adults.

The roles of adult flight and larval drift

If the number of adults represented in the sample is small, then, by chance, the offspring of these adults may not exhibit genotypic frequencies in Hardy-Weinberg equilibrium because the matings between these adults may not represent all possible matings. The element of chance may explain the erratic nature of the heterozygote deficiencies found across loci and sites.

We suggest that the tendency for local genetic differentiation in our study supports the hypothesis that nymphs collected in a particular stream were the offspring of only a few adults. Differentiation between populations on a small scale would be a result of the genotypes of the few adults populating the stream. When stream populations are pooled into subcatchments, drainages and areas, and the number of represented adults increases, this effect would be reduced and allelic differentiation would be expected to even out.

If patterns of differentiation are due to this phenomenon only, patterns between populations inhabiting different streams would be expected to be random and exhibit no relationship to the spatial arrangement of sites. The differentiation between areas at the *PepB* and *Amy* locus makes it difficult to conclude that patterns have occurred merely by chance. The genetic differentiation between areas at *PepB* and *Amy* and the lack of such differentiation at other loci may indicate that selection is acting on *PepB* and *Amy* or on closely linked loci. Selection can cause discrepancies in the patterns of genetic differentiation measured at individual loci (Slatkin 1987, Rank 1992). We cannot draw firm conclusions on the role of selection in the patterns of genetic variation observed in populations of *Baetis* sp. without further experimentation.

Although essentially a question of sampling, the possibility that the nymphs collected from a single site were the offspring of only a few adults has important implications for the effectiveness of mechanisms of stream dispersal. If the late instar nymphs collected in a stream are the offspring of only a few adults, then siblings must remain in close proximity. If siblings remain in close proximity, larval drift and other mechanisms of stream dispersal may not represent an effective means for the dispersal of *Baetis* sp. on a large scale. The abundance of *Baetis* sp. found in the drift in many studies conflicts with this explanation. However, drift rates of *Baetis* and other taxa in small rainforest streams in this region have been found to be low compared with those reported in Northern Hemisphere studies (Kerby et al. 1995). Furthermore, nymphs present in the drift may be unviable (Waters 1961, 1972) and may not establish in a new area downstream. In support of this analysis, Statzner and Bittner (1983) and Wilzbach et al. (1986) observed a relatively high incidence of parasitism in drifting invertebrates. In addition, Williams and Levins (1988) found that specimens with missing limbs constituted a greater proportion of the drift than of the benthos.

If the nymphs move little, significant differentiation between collection sites along a single stream might be expected. A tendency for greater differentiation between streams within subcatchments than at greater spatial scales has been observed in another local stream species, *Tasiagma* sp. (Trichoptera:Tasimiidae), in the same region (Hughes, unpublished). Furthermore, collections of *Tasiagma* sp. made at several reaches within a stream showed that F_{st} values between reaches were of similar magnitude to those observed among streams, and that patterns of genetic differentiation varied between loci. These results support the suggestion that, in this species, allele frequencies do not reflect gene flow between sites but may result from the genotypes of a few colonising adults. Similar work is planned for *Baetis* sp.

Acknowledgements

This project was funded in part by Grant # A19130014 from the Australian Research Council to S. E. Bunn and J. M. Hughes. Phil Suter is thanked for taxonomic assistance, as is the Queensland Forest Service and the Queensland National Parks and Wildlife Service for permission to collect. Finally, thanks to John and Ingelise Schmidt for their assistance in the field and in the preparation of the manuscript.

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Received: 15 November 1993
Accepted: 16 November 1994

APPENDIX 1. Sample sizes, allele frequencies, and observed and expected heterozygosities for each of the eight stream populations sampled.

	Population							
Locus	Branch	Stony	Scrub	Broken Bridge	Peters	Booloumba	Rum Crossing	Kilcoy
Pepb								
(N)	72	88	112	102	122	122	96	126
1	0.007	0.006	0.000	0.005	0.000	0.008	0.000	0.000
2	0.153	0.131	0.143	0.078	0.238	0.164	0.182	0.167
3	0.583	0.517	0.500	0.480	0.594	0.656	0.615	0.675
4	0.056	0.210	0.170	0.201	0.160	0.148	0.141	0.127
5	0.167	0.131	0.165	0.176	0.004	0.020	0.036	0.020
6	0.035	0.006	0.022	0.059	0.004	0.004	0.026	0.012
H(obs)	0.639	0.636	0.598	0.627	0.500	0.451	0.490	0.516
H(exp)	0.608	0.658	0.676	0.691	0.567	0.523	0.570	0.502
Mpi								
(N)	110	67	104	91	94	121	95	122
2	0.018	0.045	0.019	0.016	0.037	0.012	0.063	0.008
3	0.614	0.537	0.563	0.538	0.521	0.570	0.616	0.611
4	0.341	0.388	0.394	0.401	0.426	0.388	0.300	0.381
5	0.027	0.030	0.024	0.044	0.016	0.029	0.021	0.000
H(obs)	0.418	0.478	0.442	0.407	0.585	0.438	0.474	0.467
H(exp)	0.398	0.562	0.530	0.550	0.548	0.525	0.529	0.484
Pgi								
(N)	140	76	74	104	135	123	92	111
1	0.071	0.072	0.047	0.091	0.067	0.093	0.082	0.104
2	0.039	0.013	0.000	0.010	0.022	0.016	0.005	0.059
3	0.839	0.875	0.926	0.861	0.889	0.878	0.880	0.779
4	0.032	0.039	0.014	0.019	0.015	0.004	0.027	0.054
5	0.007	0.000	0.007	0.000	0.007	0.004	0.000	0.000
0	0.007	0.000	0.000	0.010	0.000	0.000	0.005	0.000
−1	0.004	0.000	0.007	0.010	0.000	0.004	0.000	0.005
H(obs)	0.293	0.250	0.122	0.173	0.148	0.195	0.217	0.306
H(exp)	0.289	0.229	0.142	0.252	0.205	0.221	0.219	0.377
Amy								
(N)	80	63	74	78	75	84	98	75
1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	0.188	0.238	0.203	0.109	0.133	0.101	0.061	0.127
3	0.775	0.698	0.736	0.885	0.867	0.893	0.939	0.873
4	0.038	0.063	0.061	0.006	0.000	0.006	0.000	0.000
H(obs)	0.325	0.349	0.176	0.179	0.213	0.143	0.122	0.200
H(exp)	0.365	0.455	0.416	0.207	0.233	0.194	0.116	0.223
Pgm								
(N)	129	84	95	98	108	135	94	116
1	0.000	0.000	0.005	0.000	0.023	0.004	0.016	0.013
2	0.248	0.256	0.363	0.520	0.394	0.367	0.436	0.397
3	0.450	0.387	0.468	0.332	0.426	0.348	0.367	0.422
4	0.256	0.321	0.147	0.148	0.153	0.281	0.181	0.164
5	0.047	0.036	0.016	0.000	0.005	0.000	0.000	0.004
H(obs)	0.473	0.405	0.558	0.541	0.592	0.504	0.574	0.603
H(exp)	0.671	0.684	0.630	0.600	0.643	0.668	0.646	0.640