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Influence of flow regime on life history, production, and genetic structure of *Baetis tricaudatus* (Ephemeroptera) and *Hesperoperla pacifica* (Plecoptera)

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Abstract. Life histories, annual production, and genetic structure for two insect species were examined for two adjacent streams that differ in flow regime. Birch Creek had a mesic groundwater (seasonally constant) flow regime; Little Lost River had a snowmelt (seasonally cyclic) flow regime. *Baetis tricaudatus* was multivoltine, whereas *Hesperoperla pacifica* had a life cycle longer than one year. The life histories of *B. tricaudatus* were similar between streams, but mean biomass was greater in Birch Creek. Gene frequencies of *B. tricaudatus* also were similar between streams, Nei's genetic distance being only 0.011. Expected heterozygosities and population polymorphisms were higher in the Little Lost River. In contrast, the life histories of *H. pacifica* were different between streams, emergence being later in the Little Lost River. This difference could be explained by temperature. However, the genetic structure of *H. pacifica* showed the same pattern as *B. tricaudatus* with more polymorphisms and higher heterozygosities occurring in the Little Lost River. Nei's genetic distance between the *H. pacifica* populations was 0.054. These data support the idea that populations exhibit greater genetic variability in more variable environments than populations in relatively more constant environments.

Key words: life history, population genetics, Ephemeroptera, Plecoptera, production, flow regime, disturbance.

The physical habitat is a primary controlling factor of stream benthic communities (Minshall 1988, Townsend 1989). The habitat, acting as a templet, dictates the kinds, numbers, and distributions of populations that compose stream benthic communities (sensu Southwood 1977, Poff and Ward 1989, 1990). Flow regime is an important attribute of lotic habitats that influences and constrains benthic community structure and population distributions (Lake et al. 1985, Resh et al. 1988, Wallace 1990, C. T. Robinson, unpublished data). Flow regime varies spatiotemporally, both within a system and among lotic systems (Poff and Ward 1989, 1990). This spatiotemporal habitat variability, i.e., the habitat templet, interacting with life history attributes of the population, determines the relative favorability of the habitat (Southwood 1977, 1988). For example, flow regime imposes different constraints on populations with different life histories. A seasonal flow regime may act as a disturbance to long generation (≥univoltine life cycle) populations, but may be perceived as natural environmental variation by populations with multivoltine life cycles (e.g., Resh et al. 1988, Wallace 1990).

A population life history is the phenotypic expression of the genotype interacting with the environment (Stearns 1976, Dingle and Hegmann 1982, Tauber et al. 1986). Flow regime provides the spatiotemporal variability of stream habitats that not only influences community structure but also the life histories of populations between systems (Poff and Ward 1989). One purpose of the present study was to examine the life history of two populations of aquatic insects common in two adjacent streams that differ in flow regime. Birch Creek (Birch) is a mesic groundwater stream, and the Little Lost River (Lost) is a snowmelt system according to classifications by Poff and Ward (1989). Hypothetically, these systems would be classified as being predictably constant (Birch) and predictably cyclic (Lost) (Stearns 1976).

The two populations studied from each stream were the mayfly *Baetis tricaudatus* and the stonefly *Hesperoperla pacifica*. *B. tricaudatus* was multivoltine in these streams and is considered to be an early colonist (Richards 1986, Robinson and Minshall 1986, Robinson et al. 1990). It is resilient to physical disturbance, and provides an example of a species that has adapted to adverse environmental conditions (Minshall 1988). *H. pacifica* is relatively abundant in both streams and has a generation time >1 yr. The relatively large size and long generation period of *H. pa-*

cifica should make it more susceptible to adverse flow conditions than *B. tricaudatus.*

Hedrick (1986) suggested that populations in more variable environments should express a higher degree of allelic heterozygosity and gene polymorphism than those in more stable environments (also see Nevo 1978, Hartl 1980, Parsons 1983). Consequently, life history patterns of populations in streams that differ in flow regime should have a genetic basis, and both species should exhibit greater genetic variation in the more variable Lost than in the relatively constant Birch (sensu Hedrick 1986, Pamilo 1988).

Alternatively, populations perceive environmental variation in respect to their life history, and more specifically, generation time (Southwood 1977). In general, one would expect the degree of physical habitat favorability to be temporally similar for *B. tricaudatus* and *H. pacifica* populations in Birch, whereas the degree of physical habitat favorability would be temporally different for these populations in Lost because of differences in their generation times. For example, one would predict no genetic difference (i.e., similar heterozygosity and polymorphism) between the *B. tricaudatus* populations, while heterozygosity and polymorphism should differ between *H. pacifica* populations in the two streams. *H. pacifica* should display greater levels of heterozygosity and polymorphism in Lost than in Birch because of the strong interplay between temporal variation in the habitat templet with respect to population generation time.

The primary objectives of this study were (1) to describe the life history characteristics of *B. tricaudatus* and *H. pacifica* in two adjacent streams, and (2) to compare the genetic variation of these two populations relative to the different flow regime of each stream. Starch-gel electrophoresis was used to assess genetic variation, thus this study also provides an electrophoretic survey for both species.

Study Sites

Birch and Lost are members of a group of streams collectively known as the Lost Streams of Idaho (Andrews and Minshall 1979). The Lost Streams flow from the Continental Divide towards the Snake River Plain where they sink into alluvial deposits. Consequently, the streams are physically isolated from one another. Stearns et al. (1938) suggest that the Lost Streams have been isolated from the Snake River since the early Pleistocene. The climate of this area is characterized as semi-arid with an average annual precipitation of 30 cm.

Birch and Lost are adjacent streams separated by the Lemhi Mountain Range. Study sites were chosen at about the same elevation along both streams (2083 m at Birch, and 2046 m at Lost). The Birch study site (112°57′W; 44°14′N) was about 2.0 km upstream from the town of Lone Pine, Idaho, USA. The Lost study site (113°20′W; 44°20′N) was about 150 m upstream from the mouth of Sawmill Canyon, about 65 km north of Howe, Idaho. Birch, located northeast of Lost, is bounded by the Beaverhead Mountains to the northeast. Lost is bounded to the southwest by the Lost River Mountain Range. Birch flows through a valley deeply filled (over 2745 m deep in places) with alluvium. Its principal source of water is springs (Andrews 1972). Primary riparian vegetation along Birch is river birch (*Betula fontinalis*), with sagebrush (*Artemisia*) predominant on the surrounding catchment. Balsam poplar (*Populus balsamifera*), river birch, and willow (*Salix* spp.) are common riparian vegetation along Lost, although sagebrush also is present. These two streams were chosen for the study because of their proximity to each other and their distinctly different flow regimes.

Birch was characterized chemically by higher ion concentrations (specific conductance, total hardness, alkalinity) and pH than Lost (Table 1). Marl deposits were common in Birch but absent in Lost. Nitrate (as NO_3) and ortho-phosphate values (HACH kit) were similar between sites. Mean chlorophyll *a* (mg/m^2) levels were typically higher (1–10×) in Birch than in Lost. The AFDM of periphyton also was higher (1–15×) in Birch than in Lost. Average stream widths and depths were similar between sites (Table 1). Bottom velocity tended to be higher in Birch (43–127 cm/s) than Lost (19–84 cm/s). Stream gradients were 1–3% at both study sites. Birch accumulated more annual degree days (4813) than Lost (4363), although the temporal pattern in degree day accumulation was similar between sites (Fig. 1). In addition, maximum spring temperatures were higher in Birch than in Lost.

The primary physical difference between Birch and Lost was flow regime (Fig. 1). Birch

TABLE 1. Chemical and physical characteristics of the two study streams. Annual range in values are presented for all measured parameters except mean substrata size and cumulated degree days.

Parameter	Birch	Lost
Specific conductance (μs/L)	232-350	32-130
Total hardness (mg/L $CaCO_3$)	80-200	25-65
Alkalinity (mg/L $CaCO_3$)	136-167	54-75
pH	8.5-9.0	7.2-8.8
Nitrate (as NO_3)	0.5-2.2	0.5-2.2
Ortho-phosphate (as OPO_4)	0.2-1.7	0.2-1.7
Stream width (m)	8-12	5-10
Stream depth (cm)	5-50	5-40
Bottom velocity (cm/s)	43-127	19-84
Substrata (mm)	12	18
Stream slope (%)	1-3	1-3
Degree days	4813	4363
Discharge (m^3/s)	1.16-1.65	0.001-1.37
Algal resource		
Chlorophyll *a* (mg/m^2)	2.0-42.4	0.4-19.6
AFDM (mg/m^2)	21-234	2-86

displayed a predictable constant flow regime (annual flow CV = 12%), whereas Lost was characterized by a predictable but variable flow regime (annual flow CV = 114%) (Poff and Ward 1990). Mean monthly discharge was 1.16-1.65 m^3/s in Birch and 0.001-1.37 m^3/s in Lost.

Methods

Field collections and life history determinations

Five separate riffle/run habitats were selected along a 1-2 km length of each stream on 1 January 1988. Subsequently, a random benthic sample was collected at monthly intervals at each riffle/run site using a modified Hess sampler (250 μm mesh) over a period of 16 mo. Samples were preserved with 10% formalin. A periphyton sample was collected monthly from each of the five riffle/run habitats in each stream to characterize it as a food source for *B. tricaudatus* (Richards 1986). The algal resource was quantified as chlorophyll *a* and periphyton ash-free-dry-mass (AFDM) using methods described in Robinson and Minshall (1986) (APHA 1985).

B. tricaudatus and *H. pacifica* were removed from samples using a dissecting microscope at 10× magnification. Body lengths of *B. tricaudatus* and *H. pacifica* were measured with an ocular micrometer to the nearest mm, and groups of similar-sized individuals were dried at 60°C for biomass determinations. Weights were determined with a Cahn electrobalance (Model 25) to the nearest microgram. Annual production and P/B ratios of these taxa for each stream were estimated using the size-frequency method (Hamilton 1969, Benke 1984, Benke et al. 1984). Cohorts/year were determined by life history data for *H. pacifica*, and a literature value of 2 was used for *B. tricaudatus* from populations of similar geography (Clifford 1982, Rader and Ward 1990). *Baetis* life history patterns are notoriously variable because of their extended emergence, and recruitment periods (Clifford 1982, Gaines 1987).

Monthly estimates were determined for mean density, biomass, the ratio of density/biomass (D/B), and recruitment for each taxon. The taxon D/B ratio provided an additional indication of recruitment periods. Two-way ANOVAs were completed for the above parameters on log(x + 1) transformed data using the Statistica software

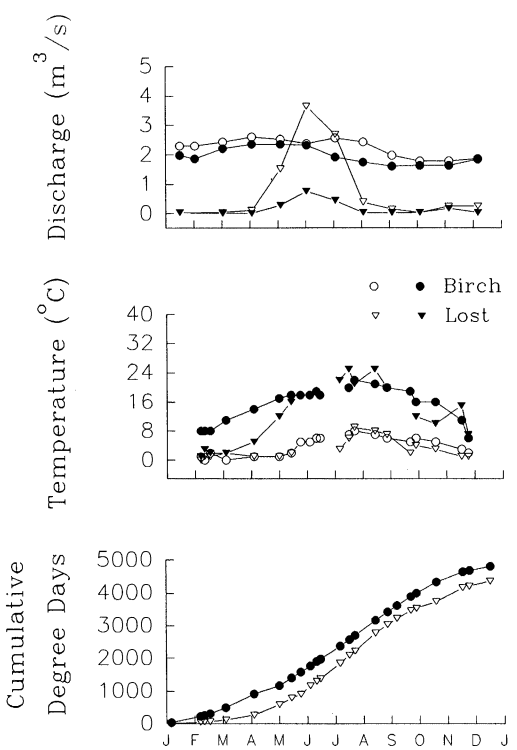

FIG. 1. Monthly maximum and minimum discharge, water temperature, and cumulated degree days for Birch Creek and Little Lost River in 1988.

package (Zar 1984, Statsoft 1990). Other statistical tests used are addressed in the text. The relative abundance of size classes by month was used to determine temporal growth patterns in life history. The period of adult emergence was estimated from these size-frequency plots.

Gel-electrophoresis

We used late-instar *B. tricaudatus* and *H. pacifica* larvae for starch gel-electrophoresis. *B. tricaudatus* larvae had well developed wing pads, whereas *H. pacifica* were selected strictly on size. *B. tricaudatus* larvae were collected from Birch and Lost in August 1988, and *H. pacifica* in December 1988 for an initial enzyme survey. Most analyses were from collections on 18 and 25 February 1989, and 1 April 1989 of both taxa. All specimens were brought to the laboratory alive and were kept alive either through refrigeration (*B. tricaudatus*) and analyzed within 2 d, or by aerating in 1-L beakers filled with water from the collection site (*H. pacifica*) and analyzed within 7 d. *H. pacifica* were held in beakers for at least 24 h to allow voiding of gut contents. The beakers with *H. pacifica* were placed in an environmental chamber to maintain relatively natural stream temperatures.

B. tricaudatus larvae were prepared for electrophoresis by grinding an entire living larva in an iced porcelain immunization depression plate using a Teflon grinding rod. Two drops of distilled water were used as a grinding medium. Individual *H. pacifica* were numbered and photographed (Kodacolor print film) for later species verification using a Minolta 35-mm (with zoom lens attachment) camera prior to grinding. These photographs also were used as representative voucher specimens. Live *H. pacifica* were ground in 0.5 mL distilled water using a Brinkman Homogenizer Model PT10/35. Specimens were kept in an ice bath to minimize enzyme denaturation during grinding.

Gel-electrophoresis of specimens was completed through an 11.5% hydrolyzed potato starch gel matrix and stained using methods of Shaw and Prasad (1970), Selander et al. (1971), and Harris and Hopkinson (1976). One individual of *H. pacifica* from each run also was analyzed on the subsequent run to act as a standard. This was not done for *B. tricaudatus* owing to the shortage of material. Several loci were assayed for both species on various buffer systems. Of 18 loci stained for *B. tricaudatus* five of these (Mdh-1, Mdh-2, a-Gpd, Hex, Pgm, Est-a, and Est-b) were homologous with those of Funk et al. (1988). Of 19 loci stained for *Hesperoperla* five (Ak, Dia++, Hex, Mdh+, and Mdh−) were homologous with Funk and Sweeney's (1990) electrophoretic study of taeniopterygid stoneflies.

TABLE 2. Summary of production values for *Baetis tricaudatus* and *Hesperoperla pacifica* in the two streams. Numbers in parentheses are standard errors of the mean.

	Annual production (P) (g/m²)	Annual P/B	Average density (No./m²)	Average biomass (B) (g/m²)
Baetis tricaudatus				
Birch	6.2	15.3	5378 (650)	0.405 (0.055)
Lost	5.7	19.5	9598 (2232)	0.293 (0.071)
Hesperoperla pacifica				
Birch	1.2	6.9	20.5 (4.9)	0.174 (0.049)
Lost	1.5	7.6	20.7 (5.1)	0.180 (0.067)

Stained gels were saved as agar overlays or wrapped in Saran Wrap™. Fluorescent gels were photographed with Tri-X Pan film using a red filter, and stained gels were photographed with (Tri-X or Ektachrome) film under Tungsten lights. Loci were scored based on relative distance of bands from the origin. Allelic frequencies, observed (H_{obs}) and expected (H_{exp}) allelic heterozygosities, population polymorphisms, and population heterozygosities were calculated from the scored loci (Ayala 1982). Sampling variances of heterozygosity were calculated using equations from Nei and Roychoudhury (1974). Deviations from Hardy-Weinberg equilibrium frequencies were examined using Chi-squared goodness-of-fit tests (Hartl 1980). Genetic identity (I) and genetic distance (D) were calculated for each species according to Nei (1978).

Results

Production estimates and life history patterns

Annual production of *B. tricaudatus* was 6.2 g/m² in Birch and 5.7 g/m² in Lost (Table 2). Annual P/B ratios for *B. tricaudatus* were 15.3 in Birch and 19.5 in Lost. Average density of *B. tricaudatus* was about 2× greater in Lost than

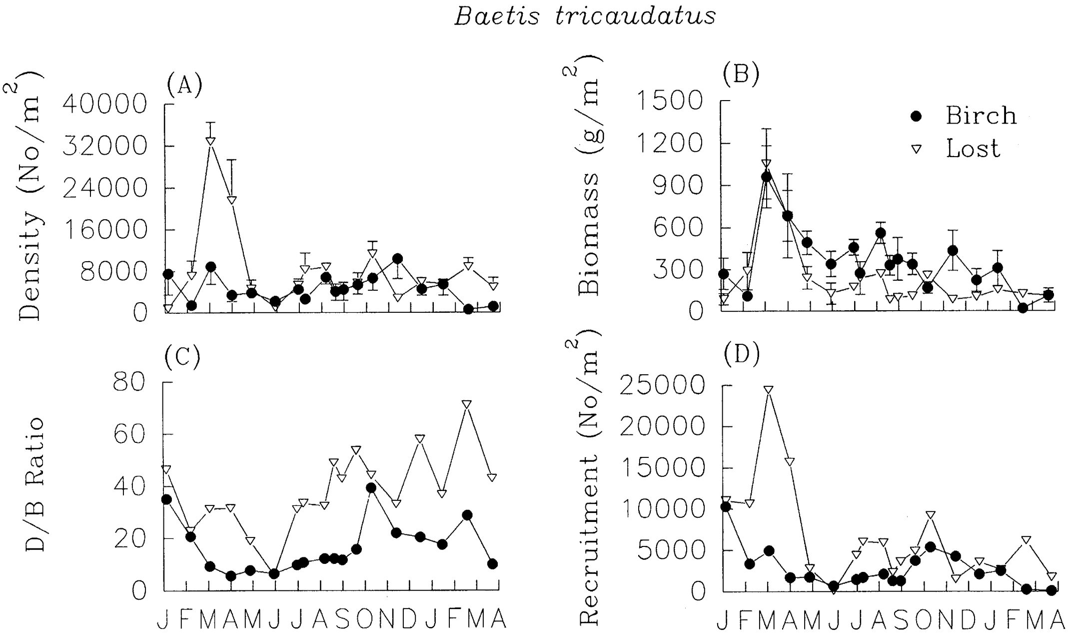

FIG. 2. Average density, biomass, density : biomass ratio, and recruitment for *Baetis tricaudatus* in Birch Creek and Little Lost River during the study period. Bars represent ±1 SD. No SD bars were placed on density : biomass ratio and recruitment graphs for clarity of seasonal patterns.

Birch, while average biomass was about 1.5× greater in Birch than Lost (Table 2). *H. pacifica* had a univoltine or longer life cycle, with annual production and P/B ratios being similar between streams. Average densities and biomasses also were similar between streams (Table 2).

B. tricaudatus displayed a significant peak ($p = 0.05$; SNK test) in numbers during late winter in Lost (Fig. 2) and abundance dropped to a seasonal low in Lost during spring runoff. No obvious patterns in abundance of *B. tricaudatus* were present in Birch (ANOVA; $p = 0.20$). The D/B ratios of *B. tricaudatus* were high (Fig. 2) compared to *H. pacifica* (Fig. 4) and fit the pattern found for other multivoltine taxa in these streams (C. T. Robinson, unpublished data). D/B ratios of *B. tricaudatus* were consistently higher in Lost than in Birch, indicating that individuals were larger in Birch. A major peak in recruitment occurred during January through April in Lost, no recruitment during spring runoff in late May and June, and continuous recruitment through summer and fall (Fig. 2). Recruitment was continous throughout the year in Birch. Life history data showed most size categories were present between January and December in 1988 (Fig. 3). Emergence occurred from late February through December in Birch and from March through late October in Lost (Fig. 3).

There was no significant difference in *H. pacifica* abundance between streams for all sampling periods ($p = 0.05$; SNK test) (Fig. 4). Biomass peaked in late winter-early spring in both systems ($p = 0.0001$), although biomass peaked earlier in Lost. The D/B ratios and recruitment data suggest recruitment occurred in fall for both streams (Fig. 4). Life history data for *H. pacifica* showed emergence occurred in April/May in Birch and May/June in Lost (Fig. 5).

Genetic heterozygosity and polymorphism

Expected allelic heterozygosity values for *B. tricaudatus* ranged from 0.00 to 0.56 in Birch (19 loci) and from 0.00 to 0.65 in Lost (18 loci examined) (Table 3). Average H_{exp} was significantly lower in Birch (0.15) than in Lost (0.21) (t-test; $p = 0.05$). Population polymorphism also was lower in Birch (42%) than in Lost (56%). Deviations from Hardy-Weinberg equilibrium were observed for two of 10 polymorphic loci (20%) in Birch and seven of 12 polymorphic loci (58%) in Lost, perhaps a result of the low sample size for some loci. Gene frequencies and H_{exp}

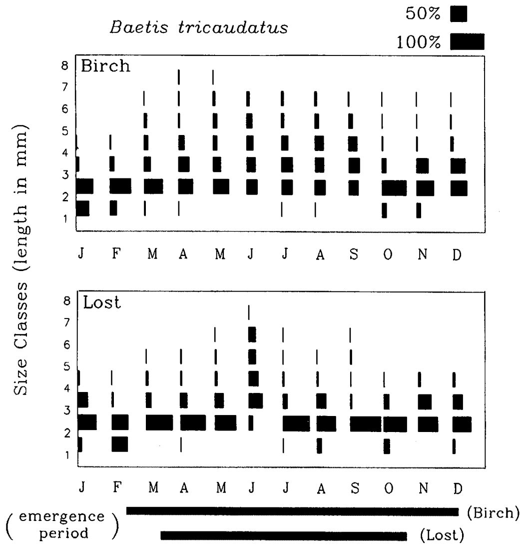

FIG. 3. Size frequency histograms by month for *Baetis tricaudatus* in Birch Creek and Little Lost River in 1988.

were quite similar for 14 loci (74%) between the two populations with the notable exceptions of EST-A, GDA, HEX-A, ICD++ and PEPala+. For example, the EST-A locus was monomorphic in Birch while being heterozygous in Lost (Table 3). The locus AK was observed in only 4 individuals from Birch. Genetic distance (D) between *B. tricaudatus* populations was 0.011 (I = 0.989).

Expected allelic heterozygosity values for *H. pacifica* ranged from 0.00 to 0.66 in Birch and from 0.00 to 0.67 in Lost for the 19 loci examined (Table 4). Average H_{exp} was significantly lower in Birch (0.20) than in Lost (0.26) (*t*-test; $p = 0.05$). Population polymorphism also was lower in Birch (53%) than in Lost (72%). Deviations from Hardy-Weinberg equilbrium were observed for seven of 12 polymorphic loci (37%) in Birch and eight of 14 polymorphic loci (42%) in Lost. Only three of these loci (HEX, ICD++, ME+) experienced similar deviations from Hardy-Weinberg between streams. In contrast to *B. tricaudatus*, gene frequencies and H_{exp} between *H. pacifica* populations were quite different for 12 loci (74% of those examined) (Table 4). Genetic distance (D) between *H. pacifica* populations was 0.054 (I = 0.946).

Discussion

The primary environmental difference between the two study streams was flow regime,

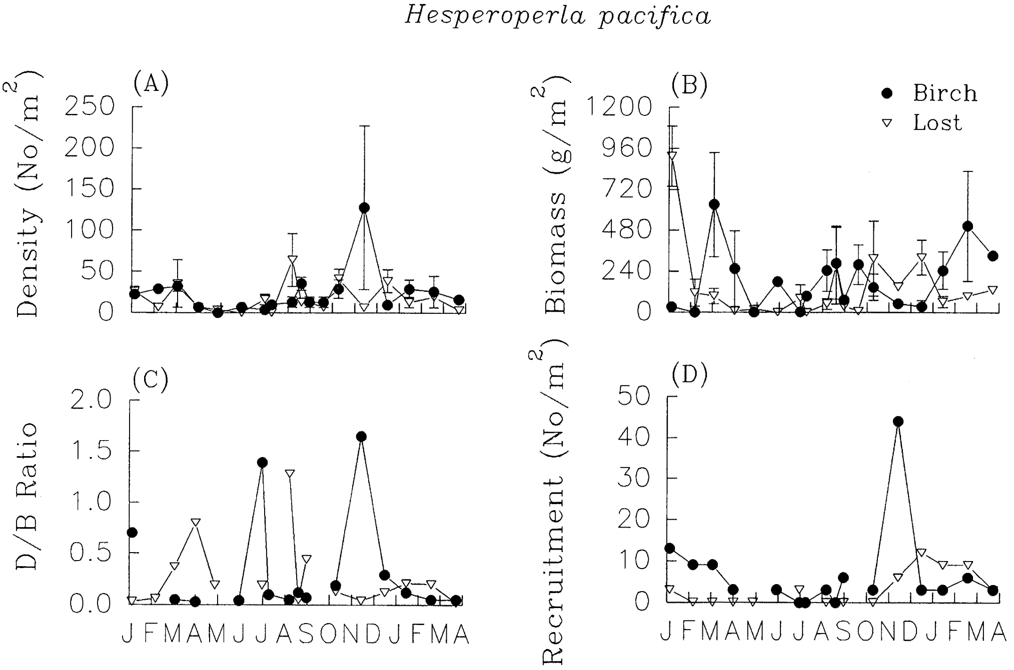

FIG. 4. Average density, biomass, density : biomass ratio, and recruitment for *Hesperoperla pacifica* in Birch Creek and Little Lost River during the study period. Bars represent ±1 SD. No SD bars were placed on density : biomass ratio and recruitment graphs for clarity of seasonal patterns.

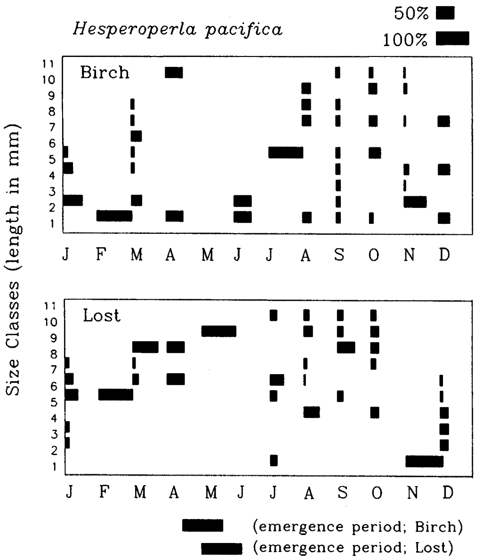

FIG. 5. Size frequency histograms by month for *Hesperoperla pacifica* in Birch Creek and Little Lost River in 1988.

although algal levels were higher in Birch. Because the study sites were located on adjacent streams and at similar elevations, other factors that could influence observed patterns were minimized or held constant. Flow regime in our study streams was geologically natural, thus providing an evolutionary basis to observed patterns in community structure and population life histories (Minshall 1988, Resh et al. 1988, Poff and Ward 1989, 1990, Wallace 1990, Fisher 1990).

Hierarchically, the study species displayed similarities in higher level properties (e.g., annual production) and differences in lower level properties (e.g., components of production) in population life histories and genetic properties between streams. For example, populations of both species exhibited similar production between streams and higher P/B ratios in Lost. Further, both species had higher expected gene heterozygosities in Lost than Birch. These data suggest that both species show some life history plasticity in response to differences in flow regime; and that general genetic properties, such as gene heterozygosity, may be similarly influenced by environmental conditions among streams. Both populations displayed greater genetic variability in Lost than those in Birch. However, the genetic response to differences in flow regime may be further modified by other environmental factors such as greater organism size resulting from enhanced food resources. Plasticity in life history allows species to maintain viable populations under different stream environments; plasticity is common among some stream insects, in particular *Baetis* spp. (Clifford 1982, Minshall 1988).

Analysis of lower level properties provided insight towards the causes of observed similarities, and consequently a better understanding of how flow regime influenced population life histories and genetic structure. In fact, the effects of flow regime can be inferred through observed life history and genetic differences among populations between the study streams. For example, although *B. tricaudatus* production was similar between streams, average density was significantly greater in Lost and average biomass greater in Birch. These data suggest that population size is maintained by greater recruitment in Lost, whereas energy is allocated to larger size in Birch. In contrast, average density and biomass of *H. pacifica* was similar between streams.

Food resources, both quality and quantity, can influence the life histories of aquatic insects (Anderson and Cummins 1979). Birch had substantially greater levels of chlorophyll *a* and periphyton AFDM than Lost suggesting greater algal abundance in Birch for grazing aquatic insects (see study area description). Enhanced food resources typically result in enhanced growth and greater sizes of macroinvertebrates (Sweeney 1984, Hart and Robinson 1990), although temperature interacts and confounds the influence of food quality and quantity on insect growth (Anderson and Cummins 1979, Sweeney et al. 1986, Resh and Rosenberg 1989). Baseflow water temperatures were similar between streams suggesting that the greater mean biomass of *B. tricaudatus* in Birch may be attributed to enhanced food resources. Hart and Robinson (1990) also found greater mean biomass for two species of algal grazers under enhanced food conditions.

Other differences in life histories between populations were found in emergence periods. Emergence of *B. tricaudatus* was earlier and longer in Birch and was not observed during spring runoff in Lost (Fig. 3). The earlier emergence

TABLE 3. Allele frequencies, observed and expected heterozygosities, number (*n*) of individuals of *Baetis tricaudatus* analyzed, and respective Chi-square (χ^2) values.

								Heterozygosity			
Locus	E.C. No.	Buffer	Site	1[a]	2	3	4	Observed	Expected	(*n*)	(χ^2)
a-GPD	1.1.1.8	T.C.8.0	Birch	0.700	0.300			0.200	0.420	5	1.37
			Lost	0.667	0.330			0.333	0.444	6	0.39
AB	fast black	LiOH	Birch	1.000				0.000		22	na
			Lost	1.000				0.000		13	na
ACON-1	4.2.1.3	T.C.8.0	Birch	0.875	0.125			0.250	0.219	8	0.16
			Lost	0.875	0.125			0.000	0.219	8	8.00*
ACON-2	4.2.1.3	T.C.8.0	Birch	1.000				0.000		15	na
			Lost	1.000				0.000		16	na
EST-A	3.1.1.1	LiOH	Birch	1.000				0.000		31	na
			Lost	0.794	0.206			0.059	0.327	17	11.42*
EST-B	3.1.1.1	LiOH	Birch	0.018	0.982			0.036	0.035	56	0.02
			Lost	0.050	0.940	0.010		0.080	0.114	50	1.85
GDA	3.5.4.3	Phos NaOH	Birch	0.011	0.978	0.011		0.044	0.043	45	1.02
			Lost	0.033	0.739	0.217	0.011	0.214	0.406	46	16.51*
HEX-A	2.7.1.1	T.C.8.0	Birch	0.012	0.395	0.523	0.070	0.302	0.565	43	53.35*
			Lost	0.011	0.391	0.391	0.206	0.347	0.652	46	45.64*
HEX-C	2.7.1.1	T.C.8.0	Birch	1.000				0.000		17	na
			Lost	1.000				0.000		12	na
AK	2.7.4.3	LiOH	Birch	1.000				0.000		4	na
			Lost							0	na
ICD+	1.1.1.42	Phos Cit 7.0	Birch	1.000				0.000		39	na
			Lost	1.000				0.000		32	na
ICD++	1.1.1.42	Phos Cit 7.0	Birch	0.833	0.167			0.267	0.278	30	0.05
			Lost	0.682	0.318			0.182	0.434	22	7.42*
LAP-1	3.4.1.1	T.C.8.0	Birch	1.000				0.000		36	na
			Lost	1.000				0.000		34	na
MDH+	1.1.1.37	Phos Cit 7.0	Birch		0.943	0.057		0.113	0.108	53	0.21
			Lost	0.026	0.974			0.052	0.051	58	0.04
MDH−	1.1.1.37	Phos Cit 7.0	Birch	1.000				0.000		39	na
			Lost	1.000				0.000		16	na
ME	1.1.1.40	Phos Cit 7.0	Birch	0.037	0.634	0.329		0.219	0.488	41	27.10*
			Lost	0.079	0.658	0.263		0.211	0.492	38	21.65*
PEPala+	3.4.11	Phos NaOH	Birch		0.579	0.421		0.460	0.488	62	0.13
			Lost	0.024	0.291	0.661	0.024	0.418	0.477	63	17.13*
PEPala−	3.4.11	Phos NaOH	Birch	1.000				0.000		46	na
			Lost	1.000				0.000		45	na
PGM	5.4.2.2	Phos NaOH	Birch		0.934	0.066		0.132	0.123	38	0.23
			Lost	0.018	0.926	0.056		0.148	0.139	27	0.73

Average heterozygosity (variance)	Observed	Expected
Birch	0.106 (0.0010)	0.146 (0.0021)*
Lost	0.114 (0.0011)	0.209 (0.0028)*
Population polymorphism (95% cutoff):	Birch 42%	Lost 56%

[a] Increase in number indicates greater distance from origin. * Significant at $p = 0.05$.

TABLE 4. Allele frequencies, observed and expected heterozygosities, number (n) of individuals of *Hesperoperla pacifica* analyzed, and respective Chi-square (χ^2) values.

Locus	E.C. #	Buffer	Site	1[a]	2	3	4	Heterozygosity Observed	Heterozygosity Expected	(n)	(χ^2)
AB	fast black	LiOH	Birch	1.000				0.000		39	na
			Lost	1.000				0.000		41	na
CAT	1.11.1.6	Phos Cit 7.0	Birch	1.000				0.000		10	na
			Lost	1.000				0.000		10	na
AK	2.7.4.3	LiOH	Birch	1.000				0.000		49	na
			Lost	1.000				0.000		51	na
dia+	1.6.*.*	Phos NaOH	Birch	0.100	0.900			0.200	0.090	10	1.45
			Lost	0.100	0.900			0.200	0.090	10	1.45
dia++	1.6.*.*	Phos NaOH	Birch			1.000		0.000		7	na
			Lost	0.250	0.063	0.688		0.500	0.460	8	2.05
EAP+	3.1.3.2	Phos Cit 7.0	Birch	0.020	0.010	0.969		0.061	0.061	49	0.89
			Lost	0.079	0.382	0.539		0.157	0.557	51	91.61*
EAP$^-$	3.1.3.2	Phos Cit 7.0	Birch	1.000				0.000		49	na
			Lost	0.961	0.039			0.000	0.075	51	51.00*
EST-B	3.1.1.1	LiOH	Birch	0.112	0.827	0.041		0.204	0.302	49	7.13*
			Lost	0.070	0.910	0.020		0.137	0.167	51	1.48
EST-D	3.1.1.1	LiOH	Birch	0.047	0.953			0.000	0.090	43	43.02*
			Lost	0.221	0.779			0.442	0.344	43	3.47
HEX	2.7.1.1	LiOH	Birch	0.022	0.056	0.333	0.589	0.067	0.539	45	58.97*
			Lost		0.141	0.295	0.564	0.102	0.575	39	48.98*
ICD+	1.1.1.42	Phos Cit 7.0	Birch	1.000				0.000		20	na
			Lost	0.850	0.150			0.000	0.255	19	19.00*
ICD++	1.1.1.42	Phos Cit 7.0	Birch	0.619	0.083	0.286	0.012	0.238	0.528	42	28.93*
			Lost	0.400	0.300	0.278	0.011	0.467	0.673	45	21.51*
MDH+	1.1.1.37	Phos Cit 7.0	Birch	0.872	0.128			0.255	0.223	47	0.96
			Lost	0.867	0.133			0.267	0.231	30	0.71
MDH−	1.1.1.37	Phos Cit 7.0	Birch	1.000				0.000		9	na
			Lost	0.929	0.071			0.000	0.132	28	28.00*
ME+	1.1.1.40	Phos Cit 7.0	Birch	0.163	0.796	0.041		0.122	0.338	49	16.11*
			Lost	0.235	0.755	0.010		0.019	0.373	51	35.73*
PEPala	3.4.11	Phos NaOH	Birch	0.289	0.710			0.053	0.414	19	14.49*
			Lost	1.000				0.000		1	na
PEPlgg	3.4.11	Phos NaOH	Birch	0.023	0.919	0.058		0.070	0.152	43	3.48
			Lost		1.000			0.000		48	na
PEPpro	3.4.11	Phos NaOH	Birch	0.333	0.278	0.389		0.330	0.661	9	10.77*
			Lost	0.200	0.350	0.450		0.900	0.635	10	2.40
PEPtyro	3.4.11	Phos NaOH	Birch	0.500	0.500			0.579	0.500	19	0.47
			Lost	0.677	0.323			0.258	0.451	31	5.49*

Average heterozygosity (variance)	Observed	Expected
Birch	0.115 (0.0013)	0.205 (0.0027)*
Lost	0.192 (0.0035)	0.264 (0.0033)*
Population polymorphism (95% cutoff):	Birch 53%	Lsot 72%

[a] Increase in number indicates greater distance from origin. * Significant at $p = 0.05$.

in Birch is probably caused by higher spring temperatures. Rader and Ward (1990) found growth rates of *B. tricaudatus* to be sensitive to differences in temperature.

H. pacifica also emerged earlier in Birch than in Lost (Fig. 5). The life history of this species is cued tightly to temperature and specifically to degree-day accumulation (J. A. Stanford, Flathead Lake Biological Station, personal communication). Birch accumulated about 500 additional degree days over Lost, mostly during spring (Fig. 1). Indeed, Birch was essentially about one month ahead of Lost in cumulative degree days and *H. pacifica* emerged about one month earlier in Birch. The lower degree day accumulation in Lost can be attributed to its flow regime being derived from snowmelt; thus water temperatures remained lower than Birch following spring thaw runoff. In effect, emergence of *H. pacifica* was synchronized not only by the cyclic flow regime in Lost, but also as a function of flow source maintaining low water temperatures in spring. This suggests the possibility that initial emergence should be more variable among years in Lost relative to Birch because of the annual variation in runoff patterns in snowmelt streams.

Few differences existed in gene frequencies for *B. tricaudatus* between streams, although population polymorphism and H_{exp} was higher in Lost. Indeed, Nei's genetic distance was quite low ($D = 0.011$) indicating little genetic differentiation and possible gene flow, by chance dispersal events, between these populations (sensu Slatkin 1985). These data support the idea that *Baetis* is a ruderal species that is highly adapted to adverse environmental conditions (Minshall 1988). *B. tricaudatus* is multivoltine and provides an example where a snowmelt flow regime acts as natural environmental variation and not a disturbance event. Indeed, coefficients of variation for average density and biomass were 84% and 87% in Lost but only 43% and 49% in Birch, respectively. In the context of this study, the snowmelt flow regime acts as a coarse-grained temporal event in respect to *B. tricaudatus* population dynamics by primarily influencing population density.

In contrast, the long generation organism, *H. pacifica*, provides an example where the snowmelt flow regime acts as a disturbance event. Although temperature explains the later emergence of *H. pacifica* in Lost, the substantial differences in gene frequencies (74%) and higher Nei's genetic distance (0.054) between populations suggest little or no gene flow (i.e., a lack of dispersal) between populations (sensu Slatkin 1985, White 1989). Further, population polymorphism was 19% greater in Lost than in Birch (Table 2). These data support the premise of higher heterozygosities and population polymorphisms in populations inhabiting more variable environments than those in relatively constant environments (Hartl 1980, Hedrick 1986). However, more research is needed to determine the relationship between generation time and environmental variation, and the consequent effect of environmental variation on the genetic structure of populations with different generation times. The life history and genetic data suggest that the flow regime of Lost is perceived by *H. pacifica* as a disturbance, but by *B. tricaudatus* as falling within the boundaries of natural environmental variation.

Although preliminary, this study provides a promising avenue towards future research into the role of the environment on population genetic structure and life histories using benthic macroinvertebrates. A number of researchers have documented increased heterozygosity with environmental variation (e.g., Nevo 1978, Zimmerman et al. 1980, Rogers and Cashner 1987) or physiological efficiency (e.g., Danzmann et al. 1987, Mitton and Lewis 1989) for a variety of organisms. Few researchers have addressed these questions for lotic macroinvertebrates (Lees and Ward 1987, Sweeney et al. 1986, 1987, Funk et al. 1988, Sweeney et al. 1992). Our study is the first we are aware of that addresses the linkage between environment and genetic structure in lotic systems. Our data suggest gene flow via migration or chance dispersal events between populations of the short generation species (*B. tricaudatus*), thus maintaining a strong species association between populations in the two streams. In contrast, the higher genetic distance and differences in gene frequencies between the *H. pacifica* populations suggest possible genetic isolation, i.e., a lack of dispersal or migration, between populations in each stream. In addition, the probability for gene flow between the *H. pacifica* populations is low because of asynchronous life histories (also see White 1989). The study streams are ideal for analyses of this sort because of their proximity and relative isolation yet contrasting physical environments. Genetic analysis provides important additional insight into the mechanics of population dynamics in relation to environmental conditions in streams.

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