Stable Isotopes Resolve the Drift Paradox for Baetis Mayflies in an Arctic River

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STABLE ISOTOPES RESOLVE THE DRIFT PARADOX FOR *BAETIS* MAYFLIES IN AN ARCTIC RIVER[1]

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Abstract. The colonization cycle hypothesis states that stream ecosystems would become depleted of insects if flying adults did not compensate for drifting immatures. Using long-term drift and benthic abundance data, we show that a *Baetis* mayfly nymph population moves downstream during development in the Kuparuk River in arctic Alaska. *Baetis* relative benthic abundance decreased from early to late season in an upstream unfertilized river section, while simultaneously increasing in the downstream fertilized section. *Baetis* nymphs drifted significantly more in the upstream unfertilized section, compared to the downstream fertilized section where food was more abundant. Approximately one-third to one-half of the nymph population drifted at least 2.1 km downstream during the arctic summer. A stable isotope tracer experiment and mathematical models show that about one-third to one-half of the adult *Baetis* population flew 1.6–1.9 km upstream from where they emerged.

These results provide a quantitative test of the colonization cycle for the dominant grazer/collector in the Kuparuk River. Quantifying the colonization cycle is essential to understanding stream ecosystem function because offspring of downstream insects are needed for nutrient cycling and carbon processing upstream. Since downstream drift and upstream flight are important components in recovery of streams from disturbances, our results provide a quantitative method for predicting recolonization rates from downstream, essential to estimating recovery.

Key words: Arctic; Baetis; *colonization cycle; drift paradox; isotope mixing model; Kuparuk River; mayflies;* [15]N; *stable isotopes; upstream flight.*

Introduction

Unidirectional transport of materials is a unique characteristic of stream ecosystems. This net transport of materials from upstream to downstream segments forms the basis of the river continuum concept (e.g., Vannote et al. 1980, Minshall et al. 1985), which has served as an important paradigm in the development of stream ecological theory. Aquatic insects and other invertebrates are important in processing organic matter as it moves downstream, affecting the abundance and size of particles (Cummins 1974, Wallace et al. 1982, Cummins et al. 1989) and the structure and function of the downstream components of the ecosystem (e.g., Vannote et al. 1980, Minshall et al. 1985).

Aquatic insects drift downstream inadvertently when

dislodged (e.g., Anderson and Lehmkuhl 1968, Wilzbach et al. 1988), and drift behaviorally to find food and avoid predators, competitors (e.g., Hildebrand 1974, Allan 1978, Peckarsky 1980, Cibrowski 1983, Kohler 1985, Malmqvist and Sjöström 1987, Flecker 1992), and pollutants (Coutant 1964, Wiederholm 1984). Downstream drift of aquatic insects presents an apparent paradox because, in spite of drift, upstream reaches are not defaunated over the long term (Müller 1954, 1982). Two hypotheses address the drift paradox: (a) Waters' excess production hypothesis states that drift represents production above carrying capacity, and sufficient numbers remain within a reach to provide adequate progeny (Waters 1972); and (b) Müller's colonization cycle hypothesis states that adult upstream flight and oviposition compensate for drift of immatures (Müller 1954, 1982). Some trapping experiments suggest that more insects fly upstream than

downstream (Müller 1954, 1982, Waters 1968), especially females (Roos 1957, Bird and Hynes 1981), but strength of evidence for upstream flight varies with taxa (Bird and Hynes 1981). Similarly, drift propensity varies considerably among taxa (e.g., Elliott 1967, Ulfstrand 1968, Lehmkuhl and Anderson 1972); thus the need for or the extent of upstream compensation also might be expected to vary. Conclusive evidence is limited that drift displacement is significant to a population (see Ulfstrand 1968, Townsend and Hildrew 1976, Müller 1982, Wilzbach and Cummins 1989). However, there are no data that relate the scale of upstream flight to the scale of downstream displacement for any population. Here, we quantify *Baetis* mayfly upstream flight in the Kuparuk River in arctic Alaska and show that the scale of adult flight is similar to our estimate of downstream displacement of nymphs.

Much mayfly drift is a behavioral response to resource availability in that food abundance within small patches provides decision criteria for drift entry (Kohler 1985, Richards and Minshall 1988). Increased algal abundance reduces *Baetis* drift on both patch (Kohler 1985) and whole-river scales (Hinterleitner-Anderson et al. 1992), indicating that *Baetis* responds to changes in algal food resources. A whole-river phosphorus fertilization experiment in the Kuparuk River in arctic Alaska has increased algal biomass, production, and consumer growth rate, and altered insect community structure (Peterson et al. 1985a, 1993, Hershey and Hiltner 1988, Hershey et al. 1988). Because *Baetis* produced a single cohort per year, hatching in late June and emerging in late July to early August, drift from upstream was the only mechanism to increase population density of *Baetis* mayfly nymphs in the fertilized section during a summer period. If the *Baetis* nymph population moved significantly in response to food abundance, drift out of the fertilized reach should have been less than drift into it; the fertilized reach should have accumulated nymphs to permit tracking of drifting mayflies. However, if drift of nymphs and upstream flight of adults are unimportant to the population, *Baetis* density could increase continually in the fertilized section over sequential summers, since adults from that section of the river lay larger eggs, which presumably have higher survivorship, than those from upstream (Hinterleitner-Anderson et al. 1992). Therefore, the fertilization experiment allowed us to determine whether drift was quantitatively important to the *Baetis* population. A ¹⁵N tracer experiment conducted in the Kuparuk River in 1991 provided an isotopic signal in the nymph and consequently in the adult population, which allowed us to quantify flight distance and direction relative to the point of emergence.

STUDY AREA

The Kuparuk River, on the North Slope of the Brooks Range in arctic Alaska, drains northward into the Arctic Ocean (described in detail in Peterson et al. 1986a,

Hershey et al., *in press*). The Kuparuk is a clear-water tundra river, having no glaciers in the watershed (Craig and McCart 1975). Our study section is a fourth-order reach, where the river crosses the Dalton Highway (formerly the Trans-Alaska Pipeline Haulroad) and the Trans-Alaska Pipeline (Fig. 1). The substrate is boulder and cobble. Permafrost is present throughout the study area at a mean depth of 40 cm in the late season (Peterson et al. 1986a) and the river itself is frozen solid during the winter. Ice-out occurs in late May to early June and the river freezes in late September or early October. Mean summer discharge ranges from 0.32 to 3.8 m³/s. The Kuparuk has been experimentally fertilized since 1983 in order to study nutrient and trophic constraints on the biotic components and nutrient cycles in the ecosystem (see Peterson et al. 1985a, 1993). *Baetis* is the only abundant mayfly in the Kuparuk River. Other common components of the insect community (the caddisfly *Brachycentrus*, black flies [Simuliidae], and chironomids) are described elsewhere (Hershey and Hiltner 1988, Hershey et al. 1988, *in press*, Peterson et al. 1993).

METHODS

Long-term fertilization of the Kuparuk River has been described previously (see Peterson et al. 1985a, 1993). Briefly, phosphoric acid was continuously dripped into the river to achieve a target PO_4-P concentration of 10 µg/L at a mean summer river discharge of 2 m³/s. This fertilization was conducted from ≈1 July to 15 August 1983–1992.

In 1991, ¹⁵N-enriched NH_4Cl was added continuously to the Kuparuk ≈1600 m upstream of the P-addition site (Fig. 1) at a constant ¹⁵N addition rate (0.89 g/d) with a peristaltic pump from 27 June to 9 August. The ¹⁵N label was rapidly incorporated into epilithic algae (an average molecule travelled 0.7 km; B. J. Peterson, *unpublished data*), a major food of *Baetis*. Tracer addition did not significantly increase NH_4^+ concentration.

Abundance of *Baetis* mayflies on the river bottom and in the drift was sampled at up to 16 stations along a 4.2-km transect of the river in the vicinity of the Trans-Alaska Pipeline Haulroad during the years 1984–1990. The number of stations sampled and the sampling frequency varied among years (Table 1). Drift samples were taken using drift nets (350-µm mesh) emplaced in the tails of riffles for 15-min intervals. Current speed was measured in front of each net approximately half-way through the sampling period using either a General Oceanics or a Marsh McBirney current meter. Discharge through each 0.139-m² net was calculated as net area times current speed over a period of 900 s. Some small instars (present during early season sampling dates) undoubtedly passed through the nets, but there was no reason to believe that sampling efficiency differed between upstream and fertilized sections, since clogging of nets was not a prob-
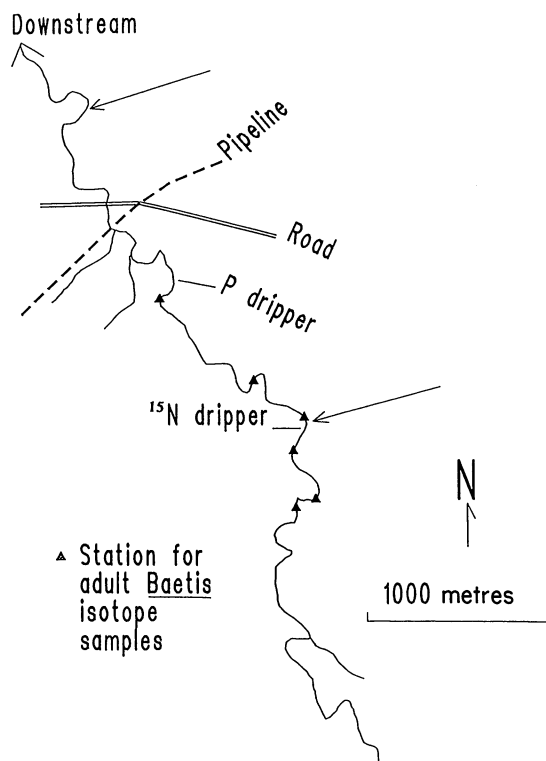
FIG. 1. Map of the study section of the Kuparuk River. Triangles (▲) indicate the locations of adult *Baetis* collections relative to the ^{15}N addition site (^{15}N dripper), the phosphorus fertilization addition site (P dripper), the Dalton Highway (Road), and the Trans-Alaska Pipeline. The arrows indicate the upstream and downstream limits of the drift and benthic sampling transects.

nymphs between river sections using two approaches. One measure of movement of the *Baetis* population between river sections is the relative drift in the upstream and fertilized sections of the river. We calculated the upstream : downstream *Baetis* drift ratio for all stations above and below the P-fertilization site. If *Baetis* drifted in proportion to their abundance, the drift ratio should be =1 if there was no fertilization effect on benthic density. If *Baetis* was more abundant in the fertilized section, and still drifted in proportion to its abundace, the drift ratio would be <1. If *Baetis* drifted more out of the upstream section, where there was less food (regardless of their relative abundance), the upstream : downstream ratio should be >1. Finally, if *Baetis* drifted randomly, the probability of a ratio >1 would equal the probability of a ratio <1. Hinterleitner-Anderson et al. (1992) showed that *Baetis* drift was a function of absolute food supply, rather than per capita food supply; thus, we hypothesized that drift would be highest in the upstream section, regardless of relative benthic density between the sites. We used a binomial test (Hollander and Wolfe 1973) to evaluate the null hypothesis that the drift ratio was unity. Another measure of the relative effect of fertilization on *Baetis* nymph movement is the ratio of downstream benthic abundance to upstream benthic abundance. *Baetis* benthic density data were examined as the ratio of densities from all stations downstream of the P-fertilization to all stations upstream of the P-fertilization on a given date. For each sampling year where comparable data existed, the downstream : upstream ratio was taken for the early season and for the late season

lem. All samples were taken between 1000 and 1700 Alaskan Standard Time (AST); however, drift shows no diurnal periodicity during the 24-h daylight of the arctic summer (Miller et al. 1986, Hinterleitner-Anderson et al. 1992), and thus there was no reason for concern about time of sampling. Three (1985–1986) or two (all subsequent years) drift samples were taken at each station (Table 1). Three (1984–1988) or two (1989) bottom samples were taken by collecting four rocks (363 ± 18 cm²) from riffles at each station, scrubbing them into a plastic basin, then concentrating the sample into a small-mesh (100 µm) net (Hershey and Hiltner 1988, Hershey et al. 1988). In late July 1984, all stations could not be sampled on any one date due to high discharge. A total of 16 stations were sampled from 24 July to 7 August, but some upstream and some fertilized stations were included on each date. These data were pooled for analyses since there was no discernible difference in abundance of *Baetis* between dates. For both drift and bottom samples, the number of samples per station was low because stations rather than samples per station were used as the unit of replication (Hershey and Hiltner 1988, Hershey et al. 1988).

We measured downstream movement of *Baetis*

TABLE 1. Number of stations sampled for drift and benthic densities of *Baetis* used to calculate benthic and drift ratios between upstream and fertilized river sections.

Date	Drift		Bottom	
	Up-stream	Down-stream	Up-stream	Down-stream
6 July 1984			3	2
24 July–7 August 1984			5	11
11 July 1985			6	4
19 July 1985	3	3		
27 July 1985			6	5
2 July 1986			6	5
13 July 1986	2	1		
25 July 1986	2	2		
3 August 1986			6	4
28 June 1987			6	6
9 July 1987			6	6
30 June 1988	4	4	7	6
13 July 1988	4	4		
25 July 1988	4	4		
27 July 1988			4	4
30 June 1990	4	4		
12 July 1990	4	4		
28 July 1990	4	4		

with respect to *Baetis* phenology in that year. The actual dates used in these calculations depended on the *Baetis* phenology each year and the dates for which samples were available. Late season for *Baetis* was defined as the last sampling date before emergence was evident. This usually occurred in late July, but in 1987, sampling was less frequent than other years, and the last sampling date prior to the onset of emergence was 9 July. If the *Baetis* population did not move or moved randomly with respect to the fertilized section of the river, we would expect to see a ratio of 1. If *Baetis* recruitment was stronger in the fertilized reach due to fertilization, we would expect to see a ratio >1 during both the early season and the late season. If *Baetis* adults flew upstream to lay eggs, and *Baetis* nymphs drifted out of the upstream section of the river where food was less abundant, into the fertilized reach, we would expect an early season ratio ≤1 and a late season ratio >1. We tested whether benthic density between downstream and upstream reaches deviated from a ratio of unity using a binomial test (Hollander and Wolfe 1973).

Movement of the adult population relative to the site of ^{15}N addition was measured during the 1991 ^{15}N enrichment experiment. Composite samples of nymphs (6–10 individuals ground together) were collected at eight sites downstream of the ^{15}N addition site just prior to peak emergence time for the population to establish the ^{15}N signal of the pre-emergent population as it peaked and decayed downstream of the ^{15}N-enrichment site. Nymphs collected from upstream (on several dates) were used to establish the baseline ^{15}N signal in the unenriched population. After emergence, composite samples of 20 adults were collected from three sites upstream and three sites downstream of the ^{15}N enrichment (Fig. 1). Adults were collected with a sweep net from the riparian zone. Swarming was not taking place at the time of sampling, and sex was not determined for individuals in each sample. Composite samples were used to integrate the variation in the ^{15}N signal between individuals; variability in sample preparation is negligible (0.1 g/kg) over the range of $\delta^{15}N$ values studied (3–250 g/kg). $\delta^{15}N$ values of adults were compared with those of nymphs to determine if the adults had moved upstream. We assumed that an adult emerging from any point along the river would have the same $\delta^{15}N$ value as a pre-emergent nymph from the same site because fractionation of ^{15}N during emergence is very unlikely to be significant. Metabolic fractionation among tissues in arthropods and rats is only 1–4 g/kg (Yoneyama et al. 1983, Schimmelmann and DeNiro 1986); thus, even if fractionation occurred between the shed nymphal exoskeleton and the retained adult tissues, the difference in nymph and adult signals would be much too small to change our conclusions since the enrichment was up to 250 g/kg. Also, since up to 90% of the material from the old cuticle is conserved during molting (see Chapman 1982), there is

no mechanism for a significant loss of either ^{15}N or ^{14}N during emergence, and thus no mechanism for a significant change in the ratio of those isotopes in the total body burden.

To identify the source distribution of adults comprising the adult samples, we used mathematical models that considered both the mixing of adult subpopulations with different $\delta^{15}N$ values, and longitudinal patterns in $\delta^{15}N$ for *Baetis* nymphs. Our models assumed that adult collections at any point d along the river comprised a mixture of an adult subpopulation emerging at point d and an adult subpopulation flying to point d from some distance away. We tested various models representing different assumptions regarding flight directions (upstream, downstream, equidirectional, or random), proportions of the subpopulations, length of stream reach over which subpopulations emerged, and the spatial variation in the nymphal $\delta^{15}N$ signal downstream.

RESULTS

Downstream drift

Our comparisons of *Baetis* drift in the upstream unfertilized and the downstream fertilized sections showed that there was more drift upstream. Actual drift densities are presented in Appendix I. On 9 of 11 dates during 4 yr, *Baetis* drift was higher upstream, where food abundance was lower, than downstream of the fertilizer addition site (Fig. 2). Thus, we rejected the null hypothesis that *Baetis* drift was equal in the two river sections ($P = .0327$, Binomial test, $n = 11$), and concluded that drift was higher in the unfertilized reach.

In the early season for *Baetis*, on or around 1 July of each year, benthic abundance was similar upstream of the P-fertilization compared to downstream ($P = .3438$, Binomial test, $n = 6$; Fig. 3). Actual benthic abundances are shown in Appendix II. Late in the season, *Baetis* abundance was ≈2–3 fold higher in the fertilized section ($P = .0156$, Binomial test, $n = 6$; Fig. 3). The distance from the midpoints of each of these river sections was 2100 m (Fig. 1). Mortality was unlikely to have been higher in the upstream section compared to the fertilized section because: (1) invertebrate predators on mayflies were essentially nonexistent (A. E. Hershey, *personal observation*); (2) grayling (*Thymallus arcticus*) were similarly abundant between river sections (B. J. Peterson, *personal observation,* and L. A. Deegan, *personal communication*); and (3) although mortality due to pathogens or parasites may be significant (Cummins and Wilzbach 1989), there is no reason to believe that these factors would be more important in the unfertilized section of the river. (In fact, fertilization of an arctic lake actually significantly enhanced parasite abundance on caddisflies [Hershey 1992].) These data suggest that the increase in nymph density during the summer was because one-third to one-half of the upstream population drifted into the fertilized
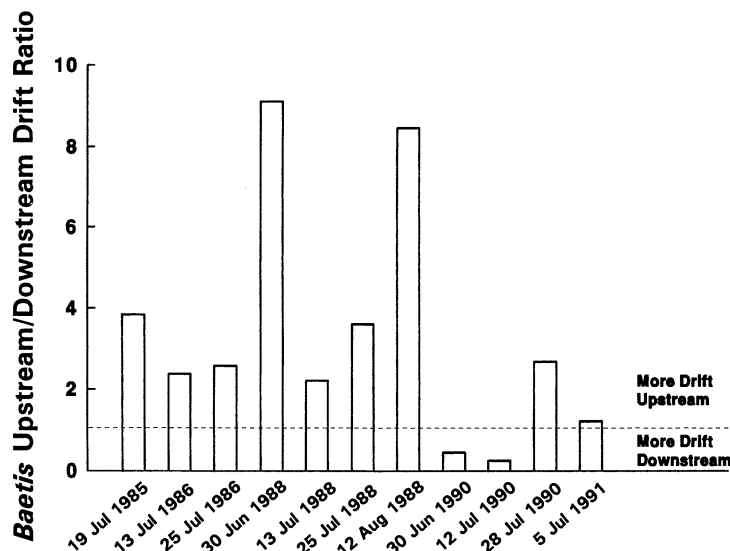
FIG. 2. Ratio of *Baetis* nymphs in the drift upstream and downstream of the fertilization site on 11 sampling dates. Upstream and downstream estimates were each means of all stations sampled on the respective date (usually four for each river section). Ratios show that drift was generally higher upstream of the fertilizer addition.

section during each summer. Furthermore, higher drift occurred in the upstream section regardless of whether *Baetis* benthic density was higher or lower there at the time of sampling (comparison of Fig. 2 and Fig. 3).

Upstream flight

Because *Baetis* abundance was as high or higher upstream than downstream at the beginning of every summer, and mayflies from the fertilized section were more abundant (Fig. 3) and carried larger eggs (Hinterleitner-Anderson et al. 1992) at the end of the preceding summer, some mechanism is needed to explain the recovery from the relatively lower abundance upstream at the end of each previous summer (Fig. 3). Upstream oviposition of adults from the fertilized section is consistent with this pattern.
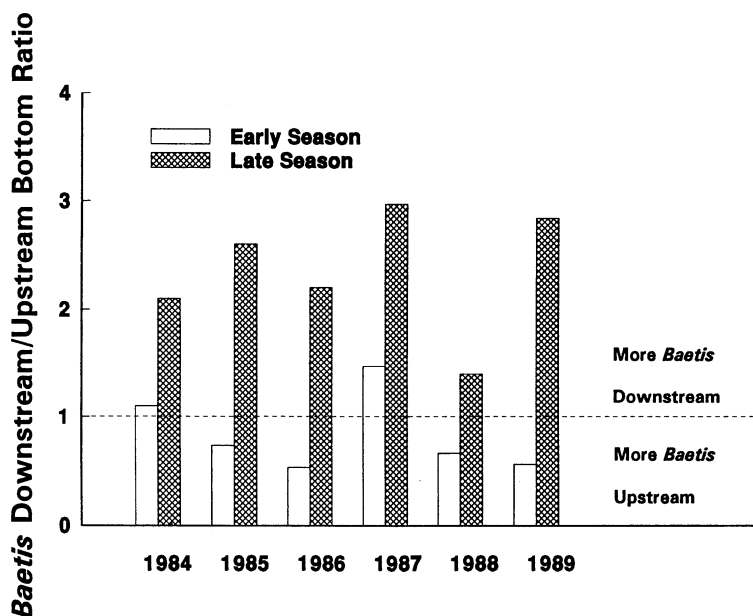

FIG. 3. Ratio of *Baetis* benthic densities in upstream and fertilized river sections in the early season, just after *Baetis* hatching, and in the late season, just prior to emergence. Ratios show that *Baetis* were more abundant downstream prior to emergence, but either equally abundant in both sections or more abundant upstream just after hatching. These results suggest that *Baetis* move downstream during the summer. To achieve equal or higher abundance upstream in the early season, some mechanism for upstream recruitment from downstream emerging adults is needed.
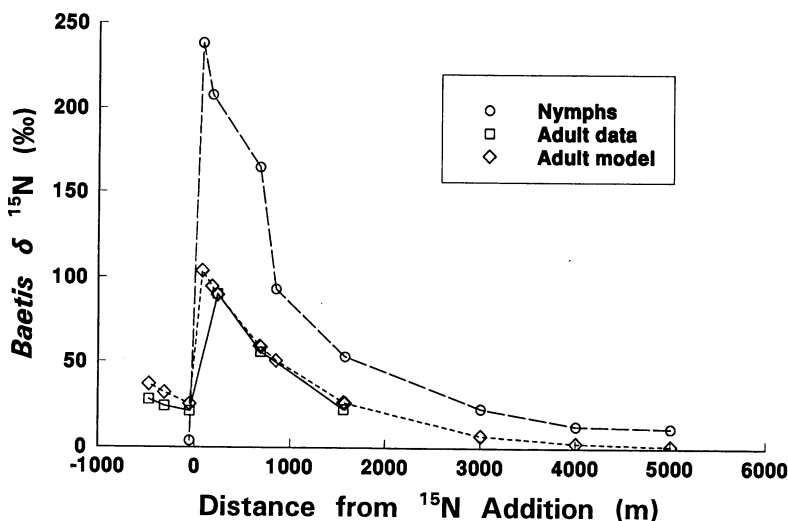
FIG. 4. Nymph and adult *Baetis* $\delta^{15}N$ upstream and downstream of the ^{15}N addition in the Kuparuk River and predictions of an adult integral mixing model (Eq. 2). Note that the "zero" point for nymphs on the x axis is from just upstream of the ^{15}N addition site (actual distance upstream was not measured). The model suggests that the adult ^{15}N signal represents an $\approx 50:50$ mixture of adults emerging from a given point and adults flying from 2 km downstream.

Patterns of changes in adult and nymphal $\delta^{15}N$ upstream and downstream of the ^{15}N source are shown in Fig. 4. The salient points of this figure that a successful model must describe are: (1) there was an exponential decline in both adult and nymphal $\delta^{15}N$ downstream of the ^{15}N addition; (2) adult mayflies were less enriched than nymphs downstream of the ^{15}N addition but more enriched upstream than upstream nymphs; (3) there was a slight but steady increase in adult $\delta^{15}N$ moving upstream from the ^{15}N addition.

The only reasonable explanation that accounts for differences in $\delta^{15}N$ between adults and nymphs is that adults collected at any one point are a mixture of adults that emerged from nymphs at that point and adults that emerged from nymphs at other points with different isotopic signals. The degree of mixing, and therefore the final signal in the adult population, is then determined by length of stream reach over which the subpopulations mixed and the relative proportions of the two subpopulations. Isotopic mixing models are commonly used to partition contributions of different sources with unique isotopic signals to a signal at a given point (DeNiro and Epstein 1981, Schoeninger et al. 1983, Peterson et al. 1985b, 1986b, Kline et al. 1990). We derived a series of models that combined elements of both isotope mixing models and models describing exponential decline in signals along gradients (Spero and Williams 1989). This family of models (Table 2) was derived as follows:

First, an exponential curve was derived to predict nymph enrichment ($\delta^{15}N_{d,N}$) d metres downstream of the source:

$$\delta^{15}N_{d,N} = \delta^{15}N_{0,N}e^{-kd} \qquad (1)$$

where $\delta^{15}N_{0,N}$ is the $\delta^{15}N$ signal in the nymphs 0 m downstream of the source (Fig. 4). This curve assumes instantaneous mixing of the added ^{15}N-NH_4; a lag in mixing (which would be ≤ 100 m; B. J. Peterson, *unpublished data*) could be accommodated by adding a constant to d. Since adults have essentially the same $\delta^{15}N$ as the nymphs from which they emerge, this equation also predicts the adult $\delta^{15}N$ at any point d metres downstream of the source at the time of emergence. The problem is to expand this equation to predict $\delta^{15}N$ of the aggregate adult swarm given different hypotheses on flight distance. These are the models in Table 2.

Accordingly, parameters ($\delta^{15}N_{0,N} = 242.5$, $k_N = 0.000925$) of this exponential curve ($r^2 = 0.998$, $P < .0001$) were inserted into the various models describing $\delta^{15}N$ of adults (Table 2). The proportions of the subpopulations (s, $1 - s$) and flight distances x and y metres downstream or upstream of d were then determined by fitting candidate equations to adult data with nonlinear parameter estimation using the Gauss–Newton procedure (Wilkinson 1990).

We considered three general subclasses of models. Each subclass incorporated the exponential decline in nymphal ^{15}N signal downstream of the source, but each differed in assumptions regarding the source of the subpopulations of adults. The simplest assumption (cloud model) is that adults emerge in a cloud described by a Poisson distribution centered on the sample point and ranging some distance x upstream and downstream from the sample point. A second set of models, the endpoint mixing models, assumed two discrete populations of adults, each with a precisely defined ^{15}N signal. One subpopulation emerges at the sampling point and the second emerges some discrete distance x away from the sample point. If x is very large, we assume

TABLE 2. Candidate mixing models describing the adult *Baetis* $\delta^{15}N$ along the longitudinal stream gradient ($\delta^{15}N_{d,A}$). s = partition coefficient of two subpopulations, d is the distance downstream or upstream from the ^{15}N source, x and y are distances of *Baetis* emergence from site d, $\delta^{15}N_{0,N}$ is the enriched $\delta^{15}N$ in nymphs at the source (= 242.5‰) and K_D is the exponential decay constant of $\delta^{15}N$ in nymphs downstream (= 0.000925). In the cloud mixing model, b, d, and f are shape parameters. NC = no convergence, RSS = residual sum of squares, $r^2 = 1 - $ RSS/total sum of squares.

Hypothesis	Model	Parameters	RSS	r^2
Cloud mixing model				
Adults emerging in a Poisson distribution x distance upstream and downstream of point d	$\delta^{15}N_{d,A} = \dfrac{b-d}{b-(d+x)} \displaystyle\int_{d-x}^{d+x} e^{-\frac{c}{f}\left(1-\frac{b-d}{b-(d+x)}\right)^f} \delta^{15}N_{0,N}e^{-kd}$	NC		
Endpoint mixing models				
Adults emerging with signal of nymphs at point d mixing with adults emerging from nymphs with background $\delta^{15}N$ = 3.6	$\delta^{15}N_{d,A} = 3.6s + (1-s)(\delta^{15}N_{0,N}e^{-k_Nd})$	s = 0.555	160.8	0.996
Adults emerging from nymphs a fixed distance x downstream of d mixing with adults emerging from nymphs with background $\delta^{15}N$ = 3.6	$\delta^{15}N_{d,A} = 3.6s + (1-s)(\delta^{15}N_{0,N}e^{-k_N}(d+x))$	s = -0.940 x = 1514	44.5	0.999
Adults emerging from nymphs a fixed distance x downstream of d mixing with adults emerging from nymphs at point d	$\delta^{15}N_{d,A} = s\delta^{15}N_{0,N}e^{-k_Nd} + (1-s)(\delta^{15}N_{0,N}e^{-k_N(d+x)})$	s = 0.30 x = 1613	90.48	0.998
Integral mixing models				
Adults with a background $\delta^{15}N$ = 3.6 mixing with adults flying to point d equal distances x upstream and downstream of d	$\delta^{15}N_{d,A} = 3.6s + (1-s)\displaystyle\int_{d-x}^{d+x} \delta^{15}N_{0,N}e^{-k_Nd}$	NC		
Adults emerging from nymphs with a background $\delta^{15}N$ = 3.6 mixing with adults emerging from nymphs in downstream reach d to $d + x$	$\delta^{15}N_{d,A} = 3.6s + (1-s)\displaystyle\int_{d}^{d+x} \delta^{15}N_{0,N}e^{-k_Nd}$	NC		
Adults emerging from nymphs at point d mixing with adults emerging from nymphs in downstream reach d to $d + x$	$\delta^{15}N_{d,A} = s\delta^{15}N_{0,N}e^{-k_Nd} + (1-s)\displaystyle\int_{d}^{d+x} \delta^{15}N_{0,N}e^{-k_Nd}$	NC		
Adults emerging from nymphs at point d mixing with adults emerging from nymphs in downstream reach $d + y$ to $d + x$	$\delta^{15}N_{d,A} = s\delta^{15}N_{0,N}e^{-k_Nd} + (1-s)\displaystyle\int_{d+y}^{d+x} \delta^{15}N_{0,N}e^{-k_Nd}$	s = 0.443 x = 1934.7 y = 1934.5	83.9	0.998

that the ^{15}N signal of the adults is equal to the background ^{15}N signal of the nymphs sampled above the ^{15}N source. A third class of models, the integral mixing models, also assumed two subpopulations of adults, but rather than assuming that adults emerge from discrete points, we instead assume that they emerge from different points along a stream reach and integrate the signal over the hypothesized reach. We believe these three subclasses of models and the variations upon each theme reasonably represent the full range of possibilities of mixing of various subpopulations of adults while still accounting for downstream declines in $\delta^{15}N$.

Models that permitted only downstream or random (cloud model in Table 2) flight either did not converge on a numerical solution, did not provide biologically reasonable parameter estimates (i.e., $s < 0$), or did not account for the greater adult ^{15}N enrichment upstream from the ^{15}N source (Table 2). An excellent fit (i.e., the lowest residual sum of squares) was given by the integral mixing model:

$$\delta^{15}N_{d,A} = s\delta^{15}N_{0,N}e^{-k_Nd}$$

$$+ (1-s)\int_{d+y}^{d+x} \delta^{15}N_{0,N}e^{-k_Nd} \quad (2)$$

where $\delta^{15}N_{0,N}$ and k_N are from Eq. 1, s = 0.443, y = 1934.5 and x = 1934.7 m downstream (r^2 = 0.998). The first term of the right-hand side of Eq. 2 is the

δ^{15}N from nymphs emerging at point d, and the second term is the δ^{15}N from nymphs emerging from a reach $d + y$ to $d + x$ metres downstream and flying upstream to point d. To test the model against the upstream adult data, we replaced the first term with 3.6 s, the δ^{15}N of the nymphs above the ^{15}N source. The model accounts for the greater δ^{15}N of adults relative to nymphs upstream; the progressive enrichment of adults upstream; the lesser enrichment of adults downstream; and the exponential decline of the adult signal downstream (Fig. 4).

The small length of stream reach over which the integral mixing model suggests that adults emerge (i.e., $x - y = 0.2$ m) indicates that an endpoint mixing model should do as well. In fact, the best endpoint mixing model (Table 2) suggests a similar partition coefficient ($s = 0.3$) and flight distance ($x = 1613$ m). Therefore, we conclude that one-third to one-half of adults preferentially fly 1.6–1.9 km upstream.

To further test convergence to a small reach, we fixed the distances x and y in Eq. 2 at various lengths, then refit the model by the same procedure. The residual sums of squares declined when integrated over larger reaches. Perhaps a finer scale of sampling would more precisely define the length of stream reach over which adults emerge. However, our qualitative conclusion derived from both integral and endpoint models remains unchanged.

Visual inspection of the adult data (Fig. 4) also supports the chosen model interpretation but not alternative models. First, the adult signal upstream of the ^{15}N source is much greater than that of unenriched nymphs. Moreover, it rises progressively upstream, whereas alternative models permitting random or equidirectional flight, which would also provide an upstream signal above background, would fall progressively upstream. Second, although the δ^{15}N signals of nymphs and adults decreased exponentially downstream from the ^{15}N source, the δ^{15}N values for adults were less than those of nymphs. This would be expected if less-enriched adults from farther downstream flew upstream, but not if more enriched adults flew preferentially downstream.

DISCUSSION

Combination of long-term fertilization and an isotopic tracer experiment with modeling provides a strong basis for resolving the drift paradox (Müller 1954, 1982, Waters 1972): downstream drift does not deplete upstream populations because it is compensated for by upstream adult flight. Resolution of the drift paradox for any population has two requirements: (1) drift must move a significant portion of the population downstream such that recruitment for the next generation would be reduced; and (2) upstream flight must occur such that the depleted population is replenished. Note that the depletion need only be very slight to shift the entire population downstream, because depletion in-

crements would accumulate through successive generations.

Our results from both drift and benthic density studies show that the Kuparuk River *Baetis* population moves downstream during its development in the arctic summer. These observations are consistent with other studies showing that *Baetis* drift from small patches of low food quality (Kohler 1985, Richards and Minshall 1988), but in this case the scale of food patch was much larger. Previous work in the Kuparuk has shown that *Baetis* drift is a function of absolute food supply, but is not density dependent (Hinterleitner-Anderson et al. 1992). In this study, we could detect the downstream movement because the experimental fertilization served as a "trap" for drifting nymphs, but in an unmanipulated river, drift effects on population movement would probably go undetected as emigrating drifters were replaced by immigrants from upstream. Also in the Kuparuk River, *Baetis* was univoltine; there was no possibility of replenishment from early instar individuals, as might occur with multivoltine populations (sensu Wilzbach and Cummins 1989). Thus, accumulation of mayflies in the fertilized section provides an illustration that small-scale behavioral events, such as drift from a food patch, can translate into large-scale population displacement. The distance between the centers of upstream and fertilized transects was 2100 m. This is a minimum estimate of the distance *Baetis* drift downstream, because if movement from upstream was much less than 2100 m, nymph accumulation in the fertilized section would have been restricted to a few stations and not have been detectable over the entire reach. However, nymphs could have drifted a greater distance and a similar accumulation would have been observed.

Allan and Feifarek (1989) have shown that the distance *Baetis* drift per event is short in artificial streams, but increases with current velocity and decreases with body size. At the maximum current velocity tested, 55 cm/s, mean drift distance ranged from 2 to 5 m (Allan and Feifarek 1989). In the Kuparuk River, current velocity through drift nets was usually in the range of 50–100 cm/s, but varied widely. Using the scenario that nymphs drift 2–5 m per drift event and move 2100 m during a 30-d development period, *Baetis* would need to drift 14–35 times/d to move this far in the Kuparuk River. At 50–100 cm/s, a nymph would spend an average of 70–140 s/d drifting to move this distance. Clearly drift displacement and depletion will vary between and within rivers depending on a variety of conditions, and depletion may be of little consequence under certain conditions (Wilzbach and Cummins 1989). Our results and conclusions are clearly restricted to *Baetis* mayflies in the Kuparuk River, and distances cannot be extrapolated to other rivers. However, the techniques we employ would be relevant to most situations.

The isotope mixing model suggests that upstream

flight of adults compensates for downstream drift of nymphs. The estimated upstream flight distance of 1.6–1.9 km is remarkably close to the 2.1 km independently estimated from drift and benthic sampling data. The partition coefficient values of the model with the best fit ($s = 0.443$ and $1 - s = 0.557$) imply that approximately half of the adults in each sample emerged in the immediate vicinity of the stream reach where a sample was taken and half emerged from ≈ 2 km downstream of the sample site. The drift and benthic density results from the fertilization experiment suggested that one-third to one-half of the nymphs drifted downstream; thus the estimate of proportions of adults engaging in compensatory flight roughly corresponds to the estimated proportion displaced downstream. Ulfstrand (1968) also estimated that one-third to one-half of a *Baetis* sp. population was displaced in the drift during its developmental period in a Lapland stream, and concluded that upstream compensation was needed. Estimates of upstream benthic movement when drift is appreciable are 6.5–7% of the population (Elliott 1971, Townsend and Hildrew 1976), too small to compensate for drift displacement, and imply that appreciable movement by adults is needed.

If partitioning is by sex, s is very close to a 50:50 sex ratio, and the model suggests that upstream flight of females only, previously observed for some stream insects (Roos 1957, Bird and Hynes 1981), could compensate for the observed downstream movement (Figs. 2 and 3) of nymphs during the growing season. Previous work in the Kuparuk shows a 50:50 sex ratio for *Baetis* (Hinterleitner-Anderson et al. 1992).

Ward (1989) suggested that application of a broad spatiotemporal perspective was essential to understanding the dynamics of pristine lotic ecosystems as well as the consequences of anthropogenic disturbance. Quantitative understanding of the colonization cycle is critical to such a spatiotemporal perspective because the upstream flight of adult insects links upstream processes to those in downstream reaches just as the River Continuum Concept (e.g., Vannote et al. 1980, Minshall et al. 1985) links downstream processes to those upstream. Because insects can control primary production and detrital decomposition, and are the major food source for stream fishes (e.g., Cummins 1974, Vannote et al. 1980, Wallace et al. 1982, Lamberti and Resh 1983, Power 1990), the colonization cycle is critical to stream ecosystem function.

Upstream flight also has significant implications for stream management. It implies that anthropogenic disturbances, such as chemical pollution, timber harvesting, or erosion, which may be deleterious to insect consumers at and downstream of their occurrence, will also impact upstream reaches. Stream ecologists have qualitatively invoked colonization by adults flying from downstream or other watersheds as important to disturbance recovery (see Wallace et al. 1986, Cairns 1990, Mackay 1992). Clearly all sources of colonizers can be important to recolonization of defaunated areas (see Williams and Hynes 1976), but recolonization by instream sources can be very limited in headwater streams (Wallace et al. 1986). Our approach provides a quantitative method to estimate recolonization from downstream, an essential step for understanding lotic ecosystems and for estimation of recovery rates in perturbed streams and rivers.

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APPENDIX I

Baetis drift densities (no./m³) used to calculate upstream/downstream drift ratios used in Fig. 2.*

Date	Upstream			Downstream		
	Mean	SE	N	Mean	SE	N
19 July 1985	1.99	0.60	3	0.52	0.13	3
13 July 1986	0.15	0.03	2	0.06	⋯	1
25 July 1986	1.06	0.30	2	0.41	0.11	3
30 June 1988	5.77	2.82	4	0.63	0.15	4
13 July 1988	1.19	0.27	4	0.54	0.21	4
25 July 1988	0.88	0.54	4	0.24	0.06	4
12 August 1988	0.45	0.10	4	0.05	0.02	4
30 June 1990	0.67	0.13	4	1.51	0.19	4
12 July 1990	0.12	0.02	4	0.47	0.09	4
28 July 1990	0.18	0.07	4	0.07	0.01	4

* Note that sampling dates differ between years depending on availability of data. Three drift nets were used at each station in 1985 and 1986, and two nets were used at each station in 1988 and 1990. *N* indicates the number of stations sampled on each date. 1988 data are from Hinterleitner-Anderson et al. (1992).

APPENDIX II

Baetis benthic densities (no./m²) used to calculate downstream : upstream ratios used in Fig. 3.*

Date	Upstream			Downstream		
	Mean	SE	N	Mean	SE	N
6 July 1984	397	45	3	427	96	2
24 July 1984	147	85	5	308	83	11
11 July 1985	1480	305	6	1077	268	4
27 July 1985	1065	217	6	2773	876	5
2 July 1986	6007	641	5	3157	408	5
3 August 1986	1321	235	6	2925	486	4
28 June 1987	549	183	6	805	195	6
9 July 1987	1996	697	6	5941	932	6
30 June 1988	4675	449	7	3074	190	6
27 July 1988	2132	394	4	3000	230	4

* Note that sampling dates differ between years depending on interannual differences in phenology and availability of comparable data. *N* = the number of stations sampled on each date. 1988 data are from Hinterleitner-Anderson et al. (1992).