Drift distance of macroinvertebrates throughout summer in headwater tributaries of the Calapooia River

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With 3 figures and 4 tables

Abstract: Drifting invertebrates from small headwater streams are a food subsidy for fishes and other downstream consumers in larger streams. This subsidy can become especially important for stream fishes during summer due to high metabolic demand caused by elevated water temperatures. The source length in small streams contributing these drifting invertebrates to fish bearing habitat has not been established. We conducted an experiment to determine if summer drift delivered by headwater streams to larger channels is influenced by contributions originating more than 100 m upstream. We conducted this experiment on tributaries of the Calapooia River, Oregon, USA. We blocked drift with 250 µm mesh nets in three streams 100 m upstream of our sample nets continuously for 48 d. We also sampled five streams without blocking nets. Four 24 h samples of drift were collected prior to the placement of blocking nets and every two weeks afterwards at each stream. Overall mean abundance and mean biomass of drift did not differ between blocked and unblocked streams for any sampling period. There was a temporal trend at all sites of declining invertebrate abundance and biomass. We found no treatment effect for any of the most common insect orders or for the 16 genera that comprised at least 1 % of the total organisms captured. The majority of invertebrate drift is of local origin in headwater streams during summer baseflow.

Key words: headwater streams, drift distance, trophic subsidy, drift density, drift type.

Introduction

Headwater streams are linked to downstream reaches along the stream network by the transport of water, organic matter, sediment, nutrients, and organisms (Gomi et al. 2002, Wipfli et al. 2007). This transported material can make an important contribution to the trophic system of larger channels (Kiffney et al. 2000). Many invertebrates use transported organic matter as a food source (Vannote 1980) and drifting invertebrates are an important food source for fishes, particularly salmonids (Elliot 1973, Fausch 1983).

Invertebrate drift rates are typically at their annual minimum during summer, low flow periods. O’Hop & Wallace (1983) found drift in winter and spring to have higher biomass than in summer in an Appalachian headwater stream. Wipfli & Gregovich (2002) found variability in 52 Alaskan headwater streams over two years, although July and August were typically the period of lowest invertebrate abundance and biomass.
in the drift. In addition to low drift rates, stream temperatures are normally high during summer, increasing the metabolic demand on consumers. As a result of low drift and high metabolic demand, food availability during summer frequently constrains fish growth in low drift and high metabolic demand, food availability of consumers. As a result of temperatures are normally high during summer, increasing metabolic demand on consumers. Therefore, invertebrate drift at this time of year, although low compared to other seasons, may be an ecologically significant component of stream food webs.

There has been considerable research on invertebrate drift (Waters 1966, Pearson & Kramer 1971, Bogatov 1984, Allan 1987), but relatively little information has been collected in a manner that would shed light on the length of headwater stream channel contributing drift at a given point downstream. Drifting invertebrates during periods of high flow may travel hundreds of meters (Neves 1970) but generally, travel covers relatively short distances under low flow conditions, approximately a few meters per drift event (Elliot 1971, Townsend & Hildrew 1976, Lancaster et al. 1996). Across species, swimming ability and size affect the distance traveled in a drift event. Chironomidae were found to drift similar distances whether they were alive or dead, indicating they were being carried passively by the current (Elliot 1971). The Ephemeropleran genus Baetis are capable swimmers and can volitionally return to the substrate, with most drifting events less than five meters (Elliot 1971). Early instars of various invertebrate species are more common in the drift than later instars (O’Hop & Wallace 1983) suggesting that these smaller individuals are more prone to enter the drift and may be carried longer distances downstream once they are drifting (Rader 1997).

The available research, however, does not provide a clear indication of where drift originates. It is possible that a relatively long length of headwater channel contributes drift to a downstream, fish-bearing reach at low flow by multiple drifting events. Even if travel during each drift event is only several meters, successive drift events may enable organisms to travel long distances. Alternatively, drift may originate primarily from reaches immediately above a site where drift is measured. Furthermore, beyond the travel dynamics, if drift represents only a small proportion of benthic population density or if reproductive rates are high, the local population would provide a sufficiently large source of invertebrates to maintain drift levels over time without supplementation from upstream. Multi-volitine species could be particularly important contributors to local population replenishment.

To determine whether drift was predominantly of local origin, we blocked drift during late summer baseflow on several small streams and compared the changes in drift density over time with that on unblocked streams. We hypothesized that if a long stream reach supported drift at a junction of a headwater channel with a larger, fish-bearing stream, then interrupting downstream drift at some point upstream of the sampling location for an extended period would produce a decline in drift density over time relative to uninterrupted sites. If drift is primarily of local origin, interrupting drift upstream should have little effect on drift density over time, relative to unblocked sites.

Material and methods

Study site selection

Our study streams were in the upper Calapooia River basin, which drains the west-slope Cascade Mountains (44 N, 122 W) in the Willamette Valley, Oregon, USA. All sites entered the mainstem, with upper and lower sites 23 km apart. The watershed receives approximately 80 cm of precipitation annually, mostly as winter rain, with summers typically dry. Mean monthly air temperature ranges from 5 to 26 °C at lower elevations in the basin. The study sites were located in an area managed for timber production and contains young to mid-aged forests composed primarily of Douglas fir (Pseudotsuga menziesii), big-leaf maple (Acer macrophyllum), and red alder (Alnus rubra).

The eight study streams were comparable in channel width and had a largely confier canopy of least 30 years of age. Streams had gradients greater than 10% with step-pool morphology. Each study stream supported continuous surface flow through the study reach and for at least a kilometer upstream of the upper end throughout the study period. The study streams were free of barriers to drifting macroinvertebrates. Each study reach was located upstream of a physical barrier to fish migration (drop of > 3 m or gradient > 20%) and was checked to ensure the streams were fishless to eliminate the possibility that differences in rates or composition among streams was because of variations in fish presence.

Five of the study streams served as reference sites and drift was uninterrupted through the study period. Morphology of the drainage networks of the study streams influenced our decision to establish study reaches of 100 m. Extending the study reaches more than 100 m would have included tributary junctions that would have complicated the experimental design. In addition, previous investigations of cumulative drift distances suggested that successive drift events over 48 d period could easily exceed 100 m (Hemsworth & Brooker 1979, Hershey et al. 1993).

Macroinvertebrate sampling

We collected macroinvertebrate drift for four sample periods at all sites at two week intervals during baseflow. Each sampling period consisted of four, 24 h drift samples from each stream. After the first sample period, we blocked drift by placing blocking nets (250-µm mesh) on three randomly chosen streams 100 m above the sampling site. Sandbags directed all water through the block nets and the nets were cleaned every 1–3 d.
depending on debris load. The block nets remained in place for 48 d, from July 17 to September 3. The four sample periods were July 13–16, August 3–6, August 16–19, and August 31 – September 3.

Drift samples were preserved in 70 % ethanol and returned to the lab for taxonomic identification, enumeration, and biomass measurements. We identified invertebrates from all samples mostly to genera (including Chironomidae). Lengths of all invertebrates, from head to end of abdomen, were measured to the nearest millimeter. In one sample from each period, we dried invertebrates in an oven at 70 °C for 12 h and measured weights to the nearest 0.0001 g with a Mettler Toledo (AG204) balance. Taxa with shells were ashed (550 °C for 6 h) after initial weighing and then reweighed. In the case of very small taxa, multiple animals were weighed together and average individual weights calculated. Weight estimates for unweighed organisms were generated from a relationship between length and weight developed from the weighed sub-sample. We combined terrestrial invertebrates in each sample, and dried and weighed those as a measure of terrestrial drift.

We classified volitionism for the 16 aquatic insect genera that comprised at least 1 % of the total number of organisms. The primary references for volitionism classifications were Poff et al. (2006), Vieira et al. (2006), and Berg & Hellenthal (2006). Two baetid mayflies (Baetis tricaudatus and Diphetor hageni), were classified as bivoltine (Poff et al. 2006). The chironomids were classified as multivoltine although bivoltinism is possible for some species (Berg & Hellenthal 1991). Other taxa, including the Dixidae, we classified as univoltine, except for Parapsyche spp., which was classified as semi-voltine (Poff et al. 2006).

Drift type by organisms is a classification based on drifting response to environmental cues or competition for space (behavioral), or by accidental entrainment in stream flow (accidental). The baetids are generally recognized as behavioral drifters with a definite diurnal pattern (Waters 1962, Kohler 1985). We considered all baetids to be behavioral drifters, although Poff et al. (2006) believed D. hageni were rare in the drift. There is conflicting information on chironomids, likely due, at least in part, to their inability to swim (Elliott 1971). However, Allan (1987), Reisen & Prins (1972), and Grzybkowska et al. (2004) classified them as behavioral drifters, and we followed that convention. Waters (1962) classified Diptera genera from the family Dixidae (Dixa and Meringodixa) as behavioral drifters. The Plecoptera genus Zapada also was classified as a behavioral drifter (Poff et al. 2006). We classified only three of the common genera as accidental drifters, the Plecoptera Yoruperla and Trichopterans Micrasema and Parapsyche (Allen 1987, Poff et al. 2006).

Characterization of physical habitat

We measured physical habitat features in September after the completion of the drift sampling. We calculated reach gradients by measuring distance and elevation, measured bankfull widths at 10 m intervals, and measured residual pool depth (Lisle 1989) for each pool.

We measured discharge at each study stream during each sampling period within 50 m of downstream net by capturing flow at a culvert outfall or waterfall. The estimate of discharge was converted to m³ d⁻¹ for use in daily drift density estimates. A remote automated weather station (RAWS) at 700 m elevation in an adjacent watershed (Brush Creek) provided daily precipitation data. After the last sampling period, we measured mean travel times by releasing a sodium chloride solution at the blocking net location and continuously measuring specific conductance at the downstream end of the reach. We calculated total stream power (Gordon et al. 1992) using gradient and mean discharge from the four sample periods. An Onset tidbit™ thermograph secured in a shaded location near the lower end of each study reach measured water temperature. Thermographs were checked for accuracy before and after deployment.

Analysis

We compared means of morphometric and hydrologic features that may influence invertebrate drift for blocked and unblocked treatment reaches with t-tests using the TTest procedure in SAS 9.1. We used the test assuming unequal variances, which is valid whether the variances are equal or unequal (Moser et al. 1992).

Drift rate for each stream for each sample period was represented by the mean abundance or biomass of the four 24 h samples. Drift density and biomass were standardized for discharge by dividing daily drift rate by 24 h discharge for each day during a sample period. We compared drift density abundance and biomass for all invertebrates, all aquatic insects, and the major orders of aquatic insects in the drift (Ephemeroptera, Plecoptera, Trichoptera, and Diptera). Drift density abundances of aquatic insect genera that comprised more than 1 % of the total sample (16 genera) also were compared.

We used repeated measures analysis of variance to test for significant differences in drift density abundance and biomass between treatment (blocked) and reference (unblocked) streams and among sample periods using the Mixed procedure in SAS 9.1. Residual plots were used to check model fit. In the few cases where transformation was warranted, there was little effect on results, so for simplicity and ease of interpretation we used data standardized for discharge in all analyses. We used the KR correction on degrees of freedom (Kenward & Roger 1997) to obtain more accurate standard errors for tests with small sample sizes (Littell et al. 2006). Akaike’s information criterion corrected (AICC) (Hurvich & Tsai 1989) was used to select the covariance structure that best fit the data from several candidate covariance structures. In almost all cases, the first-order autoregressive covariance structure (which recognizes that observations, which are closer in time, are more correlated) was the best fit and it made the most sense biologically. We used this covariance structure for all the final models. Means reported are least-squares means from the repeated measures analysis of variance.

We computed 95 % confidence limits for differences of treatment least squares means (Gerard et al. 1998) to assess the strength of the treatment comparisons for drift density abundance and biomass of overall totals and major orders. Half the difference, which is the minimum difference in the means that would be statistically significant at alpha = 0.05 given the variability and sample size.

We used lengths of the 16 common aquatic insect genera to identify possible differences in growth, presence of multivoltine generations, and perhaps asynchronous growth among sites. We identified the range of lengths of each of the common taxa during each period and combined the ranges for all sites in each period to display the range of lengths.
Results

The physical features of the study reaches between the blocked and unblocked study reaches were similar, with the exception of stream gradient (Table 1). Stream gradient was higher in the unblocked reaches; however, total stream power (p = 0.44) was not different, despite the fact that channel gradient influences this parameter. Mean discharge was similar between treatments (Table 1). During experiment site discharges were similar for sample periods 1 and 2, with a decline by sample period 3 (Fig. 1). Discharge increased at all study sites between sample periods 3 and 4 due to two storms that generated 55 mm of precipitation (Fig. 1). Tracer release studies indicated that water traveled slowly through study reaches at rates ranging from 0.26 to 0.68 m min⁻¹ and it did not differ between blocked and unblocked streams (Table 1).

Table 1. Comparisons of treatment means (t-tests) of physical characteristics of the study reaches: Blocked (n = 3) and Unblocked (n = 5).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Blocked</th>
<th>Unblocked</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bankfull width (m)</td>
<td>1.38</td>
<td>1.08</td>
<td>0.29</td>
</tr>
<tr>
<td>Residual pool depth (cm)</td>
<td>10.78</td>
<td>9.71</td>
<td>0.53</td>
</tr>
<tr>
<td>Stream gradient (%)</td>
<td>13</td>
<td>19.8</td>
<td>0.04</td>
</tr>
<tr>
<td>Mean discharge (l sec⁻¹)</td>
<td>1.64</td>
<td>1.39</td>
<td>0.59</td>
</tr>
<tr>
<td>Total stream power (watts m⁻¹)</td>
<td>0.21</td>
<td>0.28</td>
<td>0.44</td>
</tr>
<tr>
<td>Thermal maxima (T°C)</td>
<td>15.19</td>
<td>15.02</td>
<td>0.77</td>
</tr>
<tr>
<td>Time of travel (m min⁻¹)</td>
<td>0.57</td>
<td>0.44</td>
<td>0.26</td>
</tr>
</tbody>
</table>

Fig. 1. Daily precipitation (left y-axis) from nearby weather station and average daily discharge (right y-axis) during the four days of each sampling period for each site (B = Blocked, U = Unblocked).

Fig. 2. Means of drift rate abundance (ind. day⁻¹) and biomass (mg day⁻¹) for the four drift samples collected at each site (B = blocked, U = unblocked) during each sampling period (n = 4) and the contribution by major insect orders. All other macroinvertebrates are lumped as Other.
of travel was measured only after sample period 4 and likely would have been higher earlier in the experiment when discharge was higher.

Drift rates of aquatic macroinvertebrate abundance ranged from 204 to 1641 organisms day\(^{-1}\) (Fig. 2). Dry weight biomass ranged from 12 to 96 mg d\(^{-1}\) (Fig. 2). Total drift density (organisms m\(^{-3}\)) and biomass (mg m\(^{-3}\)) declined overall through time (Table 2). However, there were no differences between blocked and unblocked streams for total drift density abundance and biomass (Table 2).

Four orders (Ephemeroptera, Plecoptera, Trichoptera, and Diptera) comprised 74 and 66% of abundance and biomass of the drift, respectively. Drift density abundance of Trichoptera (\(p = 0.04\)) and drift density biomass of Ephemeroptera (\(p < 0.01\)) and

Table 2. P-values from repeated measures analysis of variance of drift density abundance and biomass for all invertebrates, aquatic invertebrates only, and the most common orders of aquatic insects in the drift. Comparisons are shown between blocked and unblocked treatments (TRT) and time (Period).

<table>
<thead>
<tr>
<th>P-value for effect</th>
<th>TRT</th>
<th>Period</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall abundance</td>
<td>0.34</td>
<td>0.001</td>
<td>0.35</td>
</tr>
<tr>
<td>Overall biomass</td>
<td>0.82</td>
<td>&lt;0.001</td>
<td>0.5</td>
</tr>
<tr>
<td>All aquatic insect abundance</td>
<td>0.48</td>
<td>&lt;0.001</td>
<td>0.12</td>
</tr>
<tr>
<td>All aquatic insect biomass</td>
<td>0.67</td>
<td>&lt;0.001</td>
<td>0.35</td>
</tr>
</tbody>
</table>

Table 3. Repeated measures analysis of variance comparison of drift density abundance for 16 common aquatic insect genera between blocked and unblocked treatments (TRT) and time (Period). Classification of genera voltinism (V: B – bivoltine, M – multivoltine, S – semi-voltine, U – univoltine) and drift type (DT: B – behavioral, A – accidental) based on review of literature (see Methods).

<table>
<thead>
<tr>
<th>Common genera</th>
<th>V</th>
<th>DT</th>
<th>% of total</th>
<th>TRT</th>
<th>Period</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baetis</td>
<td>B</td>
<td>B</td>
<td>12.8</td>
<td>0.38</td>
<td>&lt;0.01</td>
<td>0.27</td>
</tr>
<tr>
<td>Zapada</td>
<td>U</td>
<td>B</td>
<td>7.1</td>
<td>0.25</td>
<td>0.49</td>
<td>0.8</td>
</tr>
<tr>
<td>Meringodixa</td>
<td>U</td>
<td>B</td>
<td>5.9</td>
<td>0.86</td>
<td>0.38</td>
<td>0.65</td>
</tr>
<tr>
<td>Diphtheror</td>
<td>M</td>
<td>B</td>
<td>5</td>
<td>0.73</td>
<td>0.46</td>
<td>0.38</td>
</tr>
<tr>
<td>Dixa</td>
<td>U</td>
<td>B</td>
<td>4.7</td>
<td>0.27</td>
<td>0.22</td>
<td>0.59</td>
</tr>
<tr>
<td>Brillia</td>
<td>M</td>
<td>B</td>
<td>4.6</td>
<td>0.47</td>
<td>&lt;0.01</td>
<td>0.63</td>
</tr>
<tr>
<td>Ironodes</td>
<td>U</td>
<td>B</td>
<td>4.6</td>
<td>0.56</td>
<td>0.78</td>
<td>0.61</td>
</tr>
<tr>
<td>Yoraperla</td>
<td>U</td>
<td>A</td>
<td>2.9</td>
<td>0.4</td>
<td>0.17</td>
<td>0.92</td>
</tr>
<tr>
<td>Eukiefferiella</td>
<td>M</td>
<td>B</td>
<td>2.1</td>
<td>0.58</td>
<td>0.19</td>
<td>0.41</td>
</tr>
<tr>
<td>Parametriocnemus</td>
<td>M</td>
<td>B</td>
<td>1.9</td>
<td>0.75</td>
<td>0.19</td>
<td>0.88</td>
</tr>
<tr>
<td>Corynoneura</td>
<td>M</td>
<td>B</td>
<td>1.6</td>
<td>0.31</td>
<td>0.75</td>
<td>0.95</td>
</tr>
<tr>
<td>Micrasema</td>
<td>U</td>
<td>A</td>
<td>1.5</td>
<td>0.16</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Microspectra</td>
<td>M</td>
<td>B</td>
<td>1.2</td>
<td>0.92</td>
<td>0.15</td>
<td>0.37</td>
</tr>
<tr>
<td>Stempellina</td>
<td>M</td>
<td>B</td>
<td>1.2</td>
<td>0.08</td>
<td>0.48</td>
<td>0.46</td>
</tr>
<tr>
<td>Parapsyche</td>
<td>S</td>
<td>A</td>
<td>1.1</td>
<td>0.65</td>
<td>0.57</td>
<td>0.76</td>
</tr>
<tr>
<td>Tvetenia</td>
<td>M</td>
<td>B</td>
<td>1</td>
<td>0.66</td>
<td>0.17</td>
<td>0.58</td>
</tr>
</tbody>
</table>

Total 59.2
Plecoptera (p = 0.04) declined over time (Table 2). However, no differences in drift density abundance or biomass of the common orders between treatments were observed (Table 2). Sixteen aquatic insect genera comprising > 1% of total sample abundance totaled 59.2% of the total drift. None of these genera exhibited a treatment difference in drift density abundance (Table 3). Most of the common taxa showed a clear range of sizes (Fig. 3). Furthermore, we observed a range of sizes at all periods (Fig. 3). Only three genera exhibited significant differences in abundance among sample periods, *Baetis* (p = 0.003), *Brillia* (p = 0.003), and *Micrasema* (p < 0.0001), each declining in abundance through the summer (Table 3). *Micrasema* had a significant interaction of time and treatment for abundance (p = 0.001) (Table 3). This genus was twice as abundant in sample period 1 at two of three of the blocked sites but similar at those sites for the other periods. Nine of the abundant genera were Diptera and, with the exception of *Brillia*, drift density (standardized for discharge) did not decline for these genera through time (Table 3). In contrast, *Baetis*, the most abundant taxa captured, exhibited a decline in drift density through time (Table 3).

Almost half of the common genera were likely to have more than one generation per year (9 of 19) and
Drift distance of macroinvertebrates

Most were drifting behaviorally (13 of 16) (Table 3). Genera of Baetidae (2) and Chironomidae (7) likely had multiple cohorts represented during the 48 d experiment, as indicated by the range in size of the organisms captured on each sample date (Fig. 3). These taxa comprised 31.4% of the organisms collected during sampling (Table 3). The three common genera not considered behavioral drifters, Yoraperla, Micrasema, and Parapsyche, comprised 5.5% of the total drift (Table 3). The 13 common genera that were behavioral drifters accounted for 53.7% of the animals collected.

The detectable differences that our experiment could distinguish in the various categories were large compared to our observed mean treatment difference (Table 4). We found minimum detectable differences for drift density abundance and dry weight biomass of all invertebrates to be 3.22 ind. m⁻³ and 0.155 mg m⁻³, respectively (Table 4). Detectable differences for the four, most abundant aquatic invertebrate orders ranged from 0.32 to 2.36 ind. m⁻³ for abundance and 0.049 to 0.053 mg m⁻³ for biomass (Table 4).

The mean daily terrestrial drift biomass was variable, ranging from 5 to 70% of total drift biomass across all sites and periods and averaging 32%. The variability in terrestrial drift biomass was caused, in part, by the occasional capture of a few large, terrestrial invertebrates (e.g. centipedes (Chilapoda)) at some sites, which constituted a majority of the terrestrial drift biomass for these sample dates. No differences in terrestrial invertebrate biomass were seen between treatments (p = 0.529) or periods (p = 0.238).

**Discussion**

Daily drift is highly variable in streams (Brittain & Eikeland 1988) and differences among similar streams is common (Allan & Russek 1985, Wipfli & Gregovich 2002). We attempted to minimize this variability by sampling all flow for 24 h for four days during each sample period at each stream. We found no difference between blocked and unblocked headwater streams consistently across drift categories. Therefore, invertebrates more than 100 m upstream did not make a large contribution to drift during the low flow period. Rather than attributing the lack of observed differences due to just less drift, we believe these results are also a reflection of low rates of depletion relative to the size of the standing crop and adequate replenishment from growth of individuals and maybe reproduction during the 48 d. These local factors could overwhelm small differences in upstream contributions to local drift at baseflow.

The distance traveled by individual drifting organisms has been reported to range between 2 and 10 m d⁻¹ during low flow conditions (Elliott 1971, Lancaster et al. 1996). Townsend & Hildrew (1976) also found that drift distances at low flows were relatively short, estimating that 85% of individuals collected in one of their experiments originated within two meters of the sample net. Even in cases where drift was artificially encouraged, drift distances remain relatively short. McLay (1970) disturbed substrate to initiate drift, and measured travel distances ranging from 0.5 to 19.3 m. The study described here differs from previous efforts...
to determine drift distances in that we examined this process over a relatively long period of time, 48 d. This extended period and the length of our study reaches (100 m) would have allowed some organisms to travel the length of the study reach through multiple drift events, even if the distance traveled in each drift event was relatively short. Yet, elimination of the upstream contribution to drift at our blocked sites did not appear to be sufficient to decrease drift at the blocked sites.

If drift constitutes only a small proportion of the total population, a change in drift rate due to population depletion within the blocked reaches would be difficult to detect. In the larger Speed River (baseflow \(\approx 1001 \text{ sec}^{-1}\)), Bishop & Hynes (1969) estimated that only about 15 % of the annual invertebrate production left a riffle area by drift. In a stream similar in size to ours (1.4–1.9 sec\(^{-1}\)), Townsend & Hildrew (1976) found that 2.6 % of benthic invertebrates drifted from colonization trays per day. We did not measure benthic population density or biomass at our study sites. However, an estimate of the benthic population by Frady et al. (2007) from six small watersheds near our study sites found benthic invertebrate densities in June to range from 2,510 to 10,961 organisms m\(^{-2}\). If we assume the wetted width of our reaches averaged 1 m, our 100 m study reaches would support from 250,000 to 1,000,000 organisms. Our drift rates ranged from 800 to 1,700 organisms per day in Period 1 to less than 500 per day in Periods 3 and 4. Therefore, approximately 25,000 to 50,000 organisms drifted pass each sampling location over the study period. This rate of drift would constitute from 2.5 to 20 % of the benthic population, although this estimate may be somewhat low, as benthic densities from July to September would be expected to be lower than seen in the June samples of Frady et al. (2007). The estimate suggests drift was a relatively small proportion of the total benthic invertebrate population at our study sites. Therefore, depletion by drift may not have had a sufficient impact on invertebrate population to generate a detectable change in drift abundance or biomass over the study period.

Replenishment of local invertebrate populations by growth of individuals and development of multiple generations can offset depletion due to drift. Given the long period over which the treated sites were blocked, recruitment of smaller instars, even eggs, into a size class that would have been captured in the drift nets is likely. This hypothesis is supported by the range of sizes of the most common genera in the drift samples. The variation in size was likely due to several factors, including multiple species within some of the genera (e.g. Zapada spp. – four species), asynchronous growth (univoltine genera), and species with multiple generations (\(B. \text{ tricaudatus}\), various dipterans). Wilzbach & Cummins (1989) in a shorter study of blocking drift (one week), hypothesized that drift rate from a 9 m riffle would decline as the population was depleted with no replacement from upstream. They observed no decline and found that, even in a relatively short study, growth of insects from a size too small to capture into sizes available to the sampling gear was enough to maintain drift.

Population replenishment by species with multiple generations per year may have been particularly important in maintaining drift rates at our blocked sites. Bi- or multi-voltine life history has been observed in at least nine of the 16 common genera in our study: \(B. \text{ tricaudatus}\), the most abundant taxa exhibits both asynchronous growth and is bivoltine at the latitude of our study sites (Corkum & Pointing 1979). These factors together can lead to generational overlap, as was seen in \(B. \text{ tricaudatus}\) in Alberta (Clifford et al. 1973) and \(B. \text{ bicau-}
\[datus\) Dodds in Utah (Pearson & Kramer 1971). In both studies, the overlap was, in part, due to extended hatching of eggs of the spring generation, which led to asynchronous growth and reproduction.

Another possible factor augmenting populations at the study reaches is upstream dispersal by the aquatic stages of some taxa. We did not block our sites continuously at the downstream sampling location. Elliott (2003) investigated dispersal both up- and downstream of 10 genera in small streams and observed short-distance dispersals in both directions. Some upstream movement likely occurred during our study which would have occurred at blocked and unblocked sites.

Headwater streams in summer have low stream power and long times of travel. This low transport capacity is reflected in the type of drifting invertebrates we collected, as all but three of the 16 common aquatic insect genera were behavioral drifters. These three genera also were relatively uncommon in the drift, accounting for only 5.5 % of the drifting organisms captured during the study. In contrast, the 13 common genera that were behavioral drifters accounted for nearly 53.7 % of the animals collected. The majority of the drift are moving downstream in response to behavioral cues, such as lack of feeding opportunities and
avoidance of predators, providing a steady supply to downstream consumers.

Despite the low transport capacity of headwaters streams during periods of low flow, macroinvertebrate drift still occurs and at levels that suggest these systems can play a significant role in supporting the productivity of consumers in downstream reaches (Fransen et al. 1993, Bryant et al. 2004). Our result complements those of Wipfli & Gregovich (2002) suggesting that, even at low flows, headwaters streams are moving substantial numbers of invertebrates downstream and likely represent an important summer food subsidy for fishes and other predators in larger streams. In addition, our results indicate that these subsidies are largely locally derived from stream reaches in close proximity to a junction with a larger channel. Undoubtedly, drift distance will increase in streams with higher baseflow or during periods of higher discharge. Under those conditions, drift from further upstream may be carried into fish-bearing reaches.

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