The relative importance of drift causes for stream insect herbivores across a canopy gradient

Bruce G. Hammock and William C. Wetzel

B. G. Hammock (brucehammock@yahoo.com), Center for Watershed Sciences, John Muir Inst. of the Environment, Univ. of California, Davis, One Shields Avenue, Davis, CA 95616, USA. – W. C. Wetzel, Center for Population Biology, Univ. of California, Davis, Davis, CA 95616, USA.

A key attribute of riverine food webs is the downstream movement of invertebrates via the water column, or invertebrate drift. Causes of drift include benthic predation, food limitation, and perhaps passive entry, which may occur when invertebrates lose their purchase on stream substrate. However, the relative importance of drift causes is unknown, as is whether the relative importance of drift causes varies across space. Combining observational data on invertebrate herbivore and predator guild densities with in-stream experiments, we evaluated the relative importance of benthic predation, food limitation, and passive entry as proximate causes of drift for the herbivore guild across the canopy gradient of a montane stream. We found that 1) benthic predation and food limitation were both more important as causes of herbivore drift than passive entry; 2) drift caused by food limitation did not vary with riparian canopy, whereas herbivore density decreased with increasing riparian canopy, and 3) per capita drift increased linearly with increasing density, while per capita drift decreased in a negative hyperbolic fashion with increasing food, indicating that herbivore drift is proportional to herbivore density, and inversely proportional to food. We conclude that invertebrate herbivore drift was overwhelmingly an active process to improve fitness, and that herbivore food did not vary across the canopy gradient, likely because increased herbivory from larger herbivore populations at sunnier sites prevented food from accumulating.

Through their movement, animals drive a range of ecological processes, including metapopulation dynamics, gene flow, and dispersal. Animals are thought to move to increase their fitness, which foraging individuals achieve by minimizing their predation risk/foraging rate ratios (Gilliam and Fraser 1987). In streams and rivers, invertebrates commonly move downstream via the water column (Waters 1972), a process termed invertebrate drift. However, because of the presence of water current, in lotic systems it is unclear that foraging invertebrates enter the water column (move) to maximize their fitness. Instead, invertebrates may drift downstream passively as they are dislodged from the upper surfaces of substrate by the current (Elliott 1967), a hypothesis that implies no predation risk/foraging rate optimization.

Support for the passive and fitness hypotheses is mixed in streams and rivers, as are the interpretations of work to date (Allan and Castillo 2007). On one hand, considerable work demonstrates that herbivorous mayflies (Ephemeroptera), which often dominate drift samples and are frequently the focus of mechanistic drift studies (Allan 1984, Kohler 1985), actively swim into the water column to decrease their predation risk/foraging rate ratios, both in response to food limitation (Kohler 1985) and benthic predators (Peckarsky 1980). In addition, several studies found that the timing of mayfly positioning on the

upper portions of stream substrate is poorly correlated with heightened drift rates (Kohler 1983, 1985, Allan et al. 1986), contradicting a prediction of the passive drift hypothesis (Elliott 1967). On the other hand, several studies suggest that mayflies drift at a constant proportion of their population size (Walton Jr 1980, Humphries 2002, Elliott 2003), indicating that mayfly drift is a density independent process. Density independent drift is inconsistent with the hypothesis that stream invertebrate herbivores drift to increase their fitness because increasing population size decreases the amount of food per herbivore, decreasing foraging rate. Moreover, Ploskey and Brown (1980) found support for the passive drift hypothesis, Lancaster (2001) found support for both active and passive drift, James et al. (2008) and Allan and Castillo (2007) suggest that the topic is not fully resolved, and Elliott (2002) suggests that invertebrates likely drift both actively and passively. Thus, an unresolved question in stream ecology is whether stream invertebrates leave patches passively as hypothesized by Elliott (1967), or whether, as in other ecosystems, invertebrates emigrate to improve individual fitness (Bowler and Benton 2005).

The main objectives of this study were to quantify the relative importance of drift caused by predation, food limitation, and passive processes, and to determine whether the importance of those causes vary across space.

Shade from riparian vegetation can dramatically affect stream food webs (Power 1984, Doi 2009), and therefore may affect the relative importance of drift causes across a canopy gradient. We expected that invertebrate predator density would be lower in shadier, less productive sites due to decreased food for predators (Wootton and Power 1993). Therefore, because drift caused by invertebrate predators increases with predator density (Kratz 1996), we hypothesized that predation would cause higher per-capita drift of herbivores in sunnier areas. We also hypothesized that food limitation would cause greater per-capita drift of herbivores in shadier areas because food quantity (Noel et al. 1986, Hillebrand 2005) or quality (Hillebrand 2005) could be lower due to decreased productivity (Murphy 1984, Power 1984). Alternatively, herbivore density may match productivity (an ideal free distribution; Fretwell and Lucas 1969), in which case drift caused by food limitation may not decrease with canopy because increased herbivory prevents food from accumulating in sunnier locations.

We tested these hypotheses and quantified the relative importance of drift causes in a mountain stream by combining observational data with three experiments conducted in artificial channels placed in the stream. We refer to the experiments as the density, canopy and excess food experiments. In the density experiment, we measured herbivore drift from channels in which we held initial food constant and increased initial herbivore density. In the excess food experiment, we measured herbivore drift from channels in which we held initial herbivore density constant and increased initial herbivore food (predators were absent). We increased food until herbivore drift no longer decreased as food increased, thereby eliminating food limitation as a cause of drift and providing a measure of passive drift. In the canopy experiment, we quantified herbivore drift from channels containing substrate collected from 20 sites that varied in percent canopy, both with and without benthic invertebrate predators. We used the canopy experiment to test our canopy hypotheses and, in conjunction with the excess food experiment, to distinguish between the active (drift caused by food limitation and predation) and passive (e.g. drift caused by loss of footing or possibly an innate tendency to disperse) drift hypotheses.

Methods

Study site

Our study was conducted entirely in the portion of Convict Creek that runs through the Univ. of California Sierra Nevada Aquatic Research Laboratory (SNARL) near Mammoth Lakes, California, USA (37°36′57″N, 118°49′47″W). Convict Creek (elevation 2200 m) is a low gradient (slope ~2%), cobble-bottomed stream. Riparian trees and shrubs grow discontinuously along the stream creating a canopy mosaic. At the upstream end of SNARL, Convict Creek splits into three channels that meander through the reserve before converging at the downstream end of SNARL (total channel length is ~3 km). The uppermost end of the stream study section is ~4 km of stream-length downstream of Convict Lake.

Together, two mayfly taxa, *Baetis tricaudatus* and Heptageniidae, represented 88.7% of total herbivore biomass in the stream, and were therefore considered representative of the herbivore guild (Supplementary material Appendix 1).

Observational data

We randomly selected 20 sites located in either riffle or run meso-habitats distributed across the three channels of Convict Creek. We used a Surber sampler to quantify densities of invertebrate predators (length ca >3 mm) and herbivores (length ca >1.5 mm) at three randomly selected plots (20 × 20 cm) at each of the 20 sites (i.e. 60 total plots; for additional methods see Supplementary material Appendix 1). Only larger invertebrates were counted because we did not include the smallest invertebrates in our experiments (see Channel experiments for justification). The density data were used to determine whether canopy affected benthic herbivore or predator density, and to calculate mean herbivore and predator densities for Convict Creek, which provided the basis for the densities used in our canopy and food experiments. In addition, we measured percent canopy at each site using a spherical densitometer following the methodology in Herbst et al. (2009). The observational data were collected in summer 2010.

Channel experiments

We ran all of our experiments in plastic channels (1.38 m long × 0.18 m wide × 0.17 m high) placed on a concrete slab in Convict Creek using invertebrates and substrate collected from the stream (photo of channels in Supplementary material Appendix 1 Fig. A1). To make the experiments as natural as possible, we ensured that the upper surface of each cobble in the stream also faced upward in the channels and that substrate never dried before it was used in the experiments (substrate was transported from each site to the experimental channels in water-filled buckets). Treatments were randomly assigned to channels. Channels had upstream driftnets and walls that rose above the stream surface to isolate channel contents from the surrounding stream (mesh size 300 μm). We gathered substrate from various locations depending on the experiment, but for each, a similar mixture of sand, gravel and cobble was used to line the bottom of the channels. Downstream driftnets trapped drifting herbivores until they could be counted. Each channel was run for 18 h, beginning at 16:00 and ending at 10:00 the following day. We counted mayflies captured in the downstream driftnets just before sunset and just after sunrise, as well as once during the night and at the end of each channel run. The count times coincided with sunset and sunrise because invertebrate drift peaks at night in trout-bearing streams (Flecker 1992), including in Convict Creek (Hammock et al. 2012). We began our experiments during the day so that drift from the channels would initially be suppressed by the threat of diurnal trout predation, and so that by nightfall mayflies would be making drift decisions based on the conditions in the channels, rather

than drifting simply because they were disturbed by the introductions. To further minimize drift due to the introduction process, we reduced flow through the channels for ~30 s while herbivores were rinsed from collection buckets into channels, and did not include the smallest herbivores (length <1.5 mm) in our experiments. Invertebrate size is negatively correlated with diurnal drift rates because smaller invertebrates are less vulnerable to diurnal trout predation (Allan 1978). In consequence, small invertebrates would have been more likely to drift due to the introduction process. Water velocity was measured at the intake of each channel at 16:00 using a velocity meter.

We ran the density experiment to determine whether herbivore density affects herbivore drift rates in Convict Creek. It was conducted from 24 June through 28 July 2010, and had a randomized complete block design with four density treatments and seven temporal blocks (i.e. four channels were run during each temporal block, for a total of 28 channels). To begin each block, substrate was collected from sites with 100% canopy at 15:30, distributed among four channels, and herbivores were introduced to each channel at multiples of densities observed at sites with 100% canopy during summer of the previous year (0.5×, 1×, 1.5× and 2×). For the '1×' treatment, densities were 229 *Baetis tricaudatus* and 73 *Epeorus* individuals/channel (other genera in the heptageniid family were relatively rare in the stream so we used *Epeorus* in all our experiments).

The purpose of the canopy experiment was to determine whether the importance of predation and food limitation as causes of drift varied across a canopy gradient, and to determine the relative importance of drift causes. We ran the canopy experiment between 2 August and 19 September 2010 in channels using substrate collected from the same 20 sites at which the observational data were collected. We moved substrate from each of the sites (order determined randomly) and divided it equally between two channels at 15:30 (i.e. two channels were run per site, 40 channels total). Thus, the substrate in each channel had ambient levels of food for each of the 20 sites. One channel received mean densities of benthic invertebrate predators; specifically, four *Doroneuria baumanni* (Plecoptera), one *Sweltsa* (Plecoptera), two *Rhyacophila* (Trichoptera) and one Platyhelminthes. The second channel did not receive predators. We used mean densities of benthic predators because benthic predator density did not vary with canopy. At 16:00, we introduced mean densities of *B. tricaudatus* (124 individuals/channel) and *Epeorus* (89 individuals/channel) to both channels, and drifting mayflies were counted at the times listed above. However, due to the passive drift hypothesis, we could not assume that drift from channels was related to food limitation, so we also ran the excess food experiment to quantify passive drift. In addition, we counted the total number of herbivores remaining in each channel at the conclusion of the channel run so that mayflies that were missing (presumably consumed) by the end of each run could be quantified. The importance of predation as a cause of drift was determined by comparing the proportion of herbivores that drifted with benthic predators to the proportion without predators (the denominator was the total herbivores introduced). Because herbivores were consumed during the experiment, the drift proportion caused by predators is a conservative estimate.

We ran the excess food experiment to determine to what extent herbivores drift due to food limitation versus passive processes (e.g. loss of footing, innate dispersal) under baseflow conditions. Our goal was to obtain treatments consisting of six levels of herbivore food, ranging from ambient to excess food, and then to measure herbivore drift from those channels. It was run from 30 July–18 September 2010. We used a randomized complete block design with five temporal blocks. Each block consisted of six channels, and each channel contained one of six food treatments (30 channels were run in total). Because we expected herbivore food availability to increase on substrate in the absence of herbivory, the treatments consisted of substrate that had been isolated from stream herbivores in direct sunlight and flowing water for 0, 1, 2, 3, 4 and 5 24 h periods (hereafter isolation time). At 16:00 on day 6 of each block, mean densities of *B. tricaudatus* (124 individuals/channel) and *Epeorus* (89 individuals/channel) were collected from the stream and introduced to each of the six channels. We counted drift at the four times listed above. A priori, we defined 'excess food' as the isolation time at which the relationship between drift proportion and isolation time had a slope of 0, at which point we assumed that animals were not drifting due to food limitation. The substrate for the excess food experiment was collected from a single sunny site, so 'ambient food' reflected the level of food at one sunny site, rather than the entire stream (as in the canopy experiment). Following the final count, five cobbles were randomly selected from each channel and used to quantify periphyton ash-free dry mass (AFDM), which we used to determine whether periphyton increased with isolation time. We measured periphyton AFDM by scrubbing an area of 8.6 cm^2 on each of the five cobbles with a nylon brush and collecting all dislodged material onto glass fiber filters. Filters were processed for AFDM following Feminella et al. (1989).

Statistical analysis

To determine how density, food, predation risk, and percent canopy influenced rates of herbivore drift, we built generalized linear mixed models with binomial distributions and logit link functions (Bolker 2008). For each experiment, we constructed sets of models that varied in their fixed effects and represented hypothesized relationships between experimental treatments and drift rates. All models included 'experimental channel' as a random effect to account for potential correlations in drift decisions between time periods within experiment channels. We did not perform model selection on the random effect of 'channel' because it was inherent in the experimental design (Bolker 2008). We also decided a priori to use linear and quadratic terms for time as fixed effects in all models because there is a cyclical relationship between time of day and drift rates in Convict Creek (i.e. drift peaks nocturnally; Hammock et al. 2012). Based on the results of the density experiment, we included density as a fixed effect in models for the excess food and canopy experiments.

We fit models using Laplace approximation in the lme4 package (Bates et al. 2011) in R 2.14.1 (R Development Core Team). Because we were interested in drift causes for the entire herbivore guild, we did not distinguish between *B. tricaudatus* and *Epeorus* in our analyses. However, we also analyzed the taxa separately, and found that the top ranked model was the same regardless of whether taxa were analyzed together or separately (Supplementary material Appendix 2). We compared models within each experiment using sample-size corrected Akaike's information criterion (AIC$_c$; Bolker 2008). We calculated AIC$_c$ values with the sample size set to the number of experimental channels. Neither water velocity at channel intakes, which ranged from 0.46 to 0.99 m s^{-1} in our experiments, nor the temporal blocks improved the predictive ability of drift models (i.e. velocity and seasonal changes had no discernible effect on drift), so we did not include them in the analyses of our experiments.

Results

In the density experiment, the proportion of herbivores that drifted increased linearly with herbivore density (the model that included density had AIC$_c$ weight of 1.0; Table 1, Fig. 1). The parameter estimate for the slope was 0.029 (95% CI: 0.020, 0.039; note: this and other parameter estimates are on the logit scale). Mean drift proportions for each density treatment, calculated as (total drift across the four time periods)/(total introduced herbivores), were 0.14, 0.19, 0.22 and 0.25 for the 0.5×, 1×, 1.5× and 2× herbivore density treatments, respectively.

In the canopy experiment, the proportion of herbivores that drifted increased with predator presence (models that included a variable for predator presence received 100% of the AIC$_c$ weight; Fig. 2, Table 2). However, canopy had essentially no effect on herbivore drift. The top-ranked model did not include the canopy variable (Table 2), and in the model that included canopy, the effect size of increasing canopy was small (0.0045) and the 95% CI overlapped zero (−0.003, 0.012). The parameter estimate of predation was 1.84 for the top-ranked model (95% CI: 1.31, 2.37). Summed across time periods, the average proportion of herbivores that drifted from the 'predator' and 'no predator' channels were 0.53 and 0.20, respectively (proportions calculated as total drift/initial density), meaning that predator presence increased drift rates by 2.65-fold.

Table 1. Density experiment parameter estimates and Akaike's information criterion corrected for sample size (AIC$_c$) values. Linear D refers to a linear effect of density on drift proportion.

| Model | Parameter estimates (95% CIs) | | ΔAIC$_c$ | AIC$_c$ weight |
	intercept	density		
Linear D	−12.62 (−13.35, −11.89)	0.029 (0.020, 0.039)	0.0	1
Intercept	−11.34 (−11.94, −10.75)	–	35.1	0.0

Notes: Parameter estimates are on a logit scale. Though not shown, a quadratic effect of time was included in both models to account for the diel periodicity of drift.
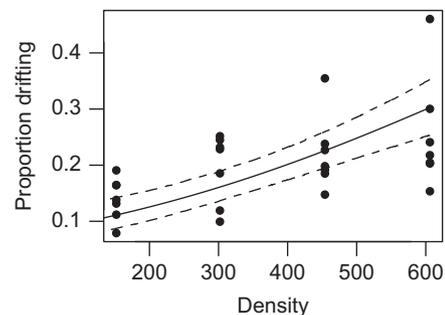

Figure 1. Results and modeling of the density experiment. The solid line is the prediction for the mean from the selected model (Table 1) and the broken lines represent the 95% confidence interval of the mean model predictions. The data and predictions are for the entire 18 h drift sampling period (16:00–10:00).

The proportion of herbivores introduced to channels that were likely consumed (i.e. mayflies that were not either counted in drift nets or in the channel the following day) was 0.11.

In the excess food experiment, the proportion of herbivores that drifted from experimental channels decreased with increasing isolation time (the two models that predicted drift proportion with a linear or quadratic effect of isolation time received 100% of the AIC$_c$ weight; Table 3). The quadratic model, in which the effect of isolation time (slope) decreased as substrate isolation time increased, received substantially more support than the linear model (97% of the AIC$_c$ weight, Table 3, Fig. 3). For the quadratic model, the parameter estimate for isolation time was −1.17 (95% CI: −1.61, −0.72), and for (isolation time)^2 the parameter estimate was 0.11 (95% CI: 0.05, 0.18). In addition, the biomass of periphyton remaining at the end of each block increased with isolation time (linear regression, $F_{1,28} = 6.59$, slope = 0.15, 95% CI ± 0.096, p = 0.0159). Average drift proportions were 0.28 from channels containing substrate with zero isolation time and 0.06 from substrate with isolation times of four and five days. Thus, average drift due to food limitation across the twenty sites in the canopy experiment (mean 'no predator' drift proportion in the canopy experiment − mean drift proportion from isolation times of 4 and 5 days in the
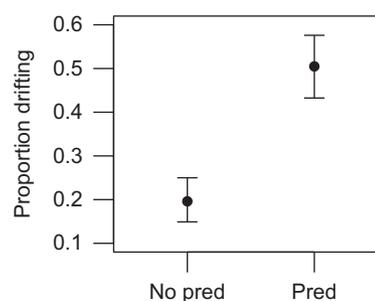

Figure 2. Results and modeling of the canopy experiment. The points represent the model predictions and 95% CI for the predator (pred) and no predator (no pred) treatments. There was not a significant effect of canopy in the experiment (Table 2). The data and predictions are for the entire 18 h drift sampling period (16:00–10:00).

Table 2. Canopy experiment parameter estimates and AIC_c values. P refers to predation and c to Canopy.

| Model | Parameter estimates (95% CIs) | | | | | ΔAIC_c | AIC_c weight |
	intercept	density	predation	canopy	predation × canopy		
P	−17.76 (−18.67, −16.85)	0.020 (0.017, 0.022)	1.84 (1.31, 2.37)	–	–	0.0	0.65
P + C	−17.98 (−18.97, −17.0)	0.020 (0.018, 0.022)	1.84 (1.32, 2.36)	0.0045 (−0.0031, 0.012)	–	1.6	0.29
P × C	−18.02 (−19.07, −16.96)	0.020 (0.018, 0.022)	1.91 (1.01, 2.81)	0.0052 (−0.0055, 0.016)	−0.0014 (−0.016, 0.014)	4.7	0.06
Intercept	−16.85 (−17.75, −15.96)	0.020 (0.018, 0.022)	–	–	–	28.0	0.0
C	−17.08 (−18.13, −16.02)	0.20 (0.018, 0.022)	–	0.0045 (−0.0067, 0.016)	–	30.2	0.0

Notes: The dash indicates that a parameter was not included in the model. Although not shown, density is included in all models because drift proportion increased with density in the density experiment (Table 1). Parameters relating drift rate to time of day are not shown. Parameter estimates are on a logit scale.

excess food experiment) was 0.136. Overall in our experiments, drift due to benthic predation, food limitation, and passive drift (but see discussion) caused drift proportions of 0.33, 0.14 and 0.06, and the mean drift rate from channels with ambient food and mean predator density was 8.8 times higher than drift from channels with excess food and no predators. Thus, under baseflow conditions, mayflies were far more likely to drift actively than passively.

Herbivore density $((Baetidae + Heptageniidae)/m^2)$ decreased with increasing percent canopy (linear regression, $F_{1,18} = 22.2$, slope = −6.9, 95% CI ± 3.1, p = 0.0002), while predator density $((D.\ baumanni + Sweltsa + Rhyacophila + Platyhelminthes + Corydalidae)/m^2)$ did not change with percent canopy (linear regression, $F_{1,18} = 0.0255$, slope = 0.02, 95% CI ± 0.21, p = 0.8956). Herbivores were roughly two times more abundant in the sunniest reaches than in the shadiest reaches (the herbivore density regression model predicts 1157 and 538 herbivores m^{-2} at canopies of 5% and 95%). Averaged across the three experiments, only 0.5% of the herbivores that were introduced to experimental channels drifted before nightfall, consistent with the summertime drift pattern in Convict Creek (i.e. largely nocturnal; Hammock et al. 2012).

Discussion

We found strong evidence that, absent from disturbance, herbivore drift in Convict Creek is largely an active process caused by food limitation and invertebrate predators. Throughout the excess food experiment, remaining periphyton increased linearly with isolation time while herbivore drift decreased with isolation time with decreasing slope. That drift rates did not change from 4 to 5 days of isolation time (i.e. the slope was 0) suggests that food limitation no longer contributed to drift in the 4 and 5 day isolation time treatments. Once food was in excess, herbivores may have drifted because individuals lost their footing as suggested by Elliott (1967), because of some innate tendency to disperse, interference competition, or injury sustained during collection. In any case, because the drift rate was far lower from the channels with excess food than from channels with natural food densities, we conclude that passive processes were not a major cause of herbivore drift.

Instead, we suggest that the proportion of herbivores that drift from patches in Convict Creek is proportional to herbivore density and predation risk, and inversely proportional to food. Holding benthic predator density constant, fitness gain (foraging rate/predation risk; Gilliam and Fraser 1987) is proportional to foraging rate, which can be expressed as herbivore food/density. Therefore, if herbivore drift from a patch is inversely proportional to fitness gain in that patch, then drift rates should increase linearly with increasing density and constant food, and decrease in a negative hyperbolic fashion with increasing food at constant density. The functional forms found in our density and excess food experiments match these predictions, as do the functional forms found in other studies that examined herbivore drift as a function of periphyton (Kohler 1985, Forrester et al. 1999). Therefore,

Table 3. Excess food experiment parameter estimates and AIC_c values. IT refers to isolation time, a parameter for the amount of time substrate was isolated from stream herbivores (i.e. allowed to accumulate food).

| Model | Parameter estimates (95% CIs) | | | | ΔAIC_c | AIC_c weight |
	intercept	density	Isolation T	(Isolation T)^2		
Quadratic IT	−14.08 (−16.27, −11.89)	0.028 (0.019, 0.037)	−1.17 (−1.61, −0.72)	0.11 (0.050, 0.18)	0.0	0.97
Linear IT	−15.06 (−17.25, −12.86)	0.028 (0.019, 0.037)	−0.39 (−0.50, −0.28)	–	6.8	0.03
Intercept	−16.48 (−18.72, −14.23)	0.028 (0.020, 0.038)	–	–	32.1	0.0

Notes: Density is included (though not shown) in all models because drift proportion increased with density in the density experiment (Table 1). Parameters relating drift rate to time of day are also not shown. Parameter estimates are on a logit scale.

because food and predation were far more important than passive processes as drift causes, and because of the functional forms of the density and food relationships, our findings are more consistent with the hypothesis that stream herbivores move to increase fitness (Gilliam and Fraser 1987) than with Elliott's (1967) passive drift hypothesis.

While we found that herbivore drift rate increased linearly with density, previous studies found no evidence that herbivore density affects herbivore drift rates (Walton Jr. 1980, Humphries 2002, Elliott 2003). However, increasing herbivore density decreases periphyton density (Lamberti et al. 1987, Hart 1987, Hillebrand 2005), and lower periphyton density increases herbivore drift (Hildebrand 1974, Kohler 1985), so there is indirect evidence suggesting that per capita drift of stream invertebrate herbivores should increase with density due to exploitative competition for food. Moreover, the analysis of the density experiment was unequivocal, and given that excluding herbivores from substrate for just one day decreased drift substantially in the excess food experiment, it seems likely that herbivores compete exploitatively for food in Convict Creek. A possible explanation for the discrepancy between the results of our experiment and previous density experiments is that we manipulated guild density, while others manipulated densities of individual taxa, possibly keeping herbivore densities below carrying capacity and keeping exploitative competition low.
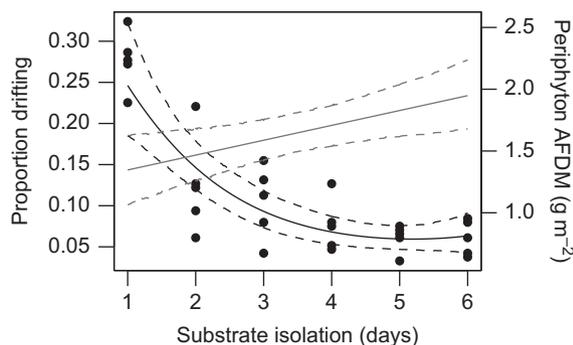

Figure 3. Results and modeling of the excess food experiment. Herbivore drift decreased in a curvilinear fashion with isolation time (Table 3), and remaining periphyton increased linearly with isolation time. The solid black line (left axis) is the mean prediction for the selected model (Table 3), and the solid gray line (right axis) is the mean prediction from a linear regression of remaining periphyton against isolation time. The broken lines are the 95% confidence intervals for the mean model predictions. The data and predictions are for the entire 18 h drift sampling period (16:00–10:00).

We found no evidence supporting our hypothesis that the drift rate of stream herbivores due to food limitation increases with increasing canopy due to lower food quantity or quality at shadier sites. Because the excess food experiment demonstrated that drift from the 'no-predator' channels in the canopy experiment was largely due to food limitation, and initial density was held constant, the canopy experiment allows us to infer from drift behavior whether food varied across the canopy gradient. Although the effect of increasing canopy on drift rates was positive as we hypothesized, the effect size was small, the confidence interval overlapped 0, and the top-ranked model by AIC_c did not include canopy. Moreover, because we used mean herbivore density rather than site specific density across the canopy gradient, and herbivores exhibited negative density dependent drift in the density experiment, our canopy experiment probably over-estimated the positive effect of canopy on drift. It also appeared that food quality did not vary appreciably across the canopy gradient, inconsistent with Hillebrand (2005). We conclude that canopy cover did not affect standing food biomass significantly.

Instead, our results are more consistent with the alternative hypothesis that, because herbivore densities in sunnier stream reaches were higher, herbivores consumed periphyton at a higher rate. By consuming more food, herbivores presumably offset the increased productivity at sunnier sites, keeping food availability at a similar level across the canopy gradient. This is the same conclusion that Power (1983) drew from observations that periphyton density was equal across a canopy gradient, while periphyton productivity and herbivorous catfish density decreased with canopy in a neotropical stream. Power (1983) also demonstrated that catfish density closely matched periphyton productivity across a canopy gradient, and concluded that the catfish exhibited an ideal free distribution (Fretwell and Lucas 1969). In our study, food level and benthic predator density were equal across a canopy gradient, but herbivore density decreased with increasing canopy. Therefore, it seems likely that herbivore density in Convict Creek also matched periphyton productivity, and that herbivores distributed themselves such that feeding rates were equal across the canopy gradient.

Like food availability, the effect of predators on drift rates did not vary with canopy, simply because predator density did not vary with canopy. One explanation for why predator density did not vary is that mayflies may not comprise a substantial proportion of the diet of invertebrate predators. So while mayfly density appeared to track productivity, invertebrate predators did not track mayfly density in turn. The density of invertebrate predators may

instead be driven by prey that are less affected by canopy (e.g. filter feeders), or that were not included in our experiments (e.g. Chironomidae). A second possibility is that the higher trophic level (trout) prevented invertebrate predators from moving to the patches with the highest food density (Feltmate and Williams 1989).

One concern regarding the canopy experiment is that we prevented immigration into the channels, causing population sizes of channels to drop as herbivores emigrated, potentially affecting the importance of food limitation and benthic predation as causes of drift. However, a study by Kratz (1996), also conducted in Convict Creek, demonstrated that per capita drift of *B. tricaudatus* in the presence of *D. baumanni* was not influenced by the density of *B. tricaudatus*. Thus, we consider it unlikely that the effect size of predation was strongly affected by herbivore density. We are more concerned that we underestimated the importance of food limitation as a cause of drift. The density experiment demonstrates that per capita drift decreases with decreasing density, likely because of a decrease in exploitative competition for food. Therefore, the drift rate from the 'no predator' channels in the canopy experiment (which contained ambient food) may be an underestimate of the actual proportion of drift induced by food limitation in Convict Creek.

Overall, we conclude that, absent from disturbance, herbivore drift in Convict Creek at baseflow is predominantly caused by invertebrate predators and food limitation, and is therefore an active behavior to improve fitness. From the perspective of the herbivores, food level was equal across the canopy gradient, likely because larger populations at sunnier sites offset increased productivity. Finally, we found strong evidence for density dependent movement, likely due to exploitative competition among stream herbivores. Overall, our results are far more consistent with the general hypothesis that mayflies move among patches to maximize fitness (Gilliam and Fraser 1987) than with the passive drift hypothesis (Elliott 1967).

References

Allan, J. D. 1978. Trout predation and the size composition of stream drift. – Limnol. Oceanogr. 23: 1231–1237.

Allan, J. D. 1984. The size composition of invertebrate drift in a Rocky Mountain Colorado USA stream. – Oikos 43: 68–76.

Allan, J. D. and Castillo, M. M. 2007. Stream ecology: structure and function of running waters. – Springer.

Allan, J. et al. 1986. Diel epibenthic activity of mayfly nymphs, and its nonconcordance with behavioral drift. – Limnol. Oceanogr. 31: 1057–1065.

Bates, D. et al. 2011. lme4: Linear mixed-effects models using S4 classes. – R package ver. 0.999375-42 <http://CRAN.R-project.org/package = lme4>

Bolker, B. M. 2008. Ecological models and data in R. – Princeton Univ. Press.

Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – Biol. Rev. 80: 205–225.

Doi, H. 2009. Spatial patterns of autochthonous and allochthonous resources in aquatic food webs. – Popul. Ecol. 51: 57–64.

Elliott, J. M. 1967. Invertebrate drift in a Dartmoore stream. – Arch. Hydrobiol. 63: 202–237.

Elliott, J. M. 2002. A continuous study of the total drift of freshwater shrimps, *Gammarus pulex*, in a small stony stream in the English Lake District. – Freshwater Biol. 47: 75–86.

Elliott, J. M. 2003. A comparative study of the dispersal of 10 species of stream invertebrates. – Freshwater Biol. 48: 1652–1668.

Feltmate, B. W. and Williams, D. D. 1989. Influence of rainbow trout (*Oncothynchus mykiss*) on density and feeding behaviour of a perlid stonefly. – Can. J. Fish. Aquat. Sci. 46: 1575–1580.

Feminella, J. W. et al. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. – Freshwater Biol. 22: 445–457.

Flecker, A. S. 1992. Fish predation and the evolution of invertebrate drift periodicity: evidence from Neotropical streams. – Ecology 73: 438–448.

Forrester, G. E. et al. 1999. Trophic interactions in open systems: effects of predators and nutrients on stream food chains. – Limnol. Oceanogr. 44: 1187–1197.

Fretwell, S. D. and Lucas, H. L. 1969. On territorial behavior and other factors influencing habitat distribution in birds. – Acta Biotheor. 19: 16–36.

Gilliam, J. F. and Fraser, D. F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. – Ecology 68: 1856–1862.

Hammock, B. G. et al. 2012. Incorporating invertebrate predators into theory regarding the timing of invertebrate drift. – Aquat. Ecol. 46: 153–163.

Hart, D. D. 1987. Experimental studies of exploitative competition in a grazing stream insect. – Oecologia 73: 41–47.

Herbst, D. B. et al. 2009. The influence of introduced trout on the benthic communities of paired headwater streams in the Sierra Nevada of California. – Freshwater Biol. 54: 1324–1342.

Hildebrand, S. G. 1974. The relation of drift to benthos density and food level in an artificial stream. – Limnol. Oceanogr. 19: 951–957.

Hillebrand, H. 2005. Light regime and consumer control of autotrophic biomass. – J. Ecol. 93: 758–769.

Humphries, S. 2002. Dispersal in drift-prone macroinvertebrates: a case for density-independence. – Freshwater Biol. 47: 921–929.

James, A. et al. 2008. The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. – River Res. Appl. 24: 22–35.

Kohler, S. L. 1983. Positioning on substrates, positioning changes, and diel drift periodicities in mayflies. – Can. J. Zool. 61: 1362–1368.

Kohler, S. L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. – Ecology 66: 1749–1761.

Kratz, K. W. 1996. Effects of stoneflies on local prey populations: mechanisms of impact across prey density. – Ecology 77: 1573–1585.

Lamberti, G. A. et al. 1987. Herbivory and intraspecific competition in a stream caddisfly population. – Oecologia 73: 75–81.

Lancaster, J. 2001. Small-scale movements of lotic macroinvertebrates with variations in flow. – Freshwater Biol. 41: 605–619.

Murphy, M. L. 1984. Primary production and grazing in freshwater and intertidal reaches of a coastal stream, southeast Alaska. – Limnol. Oceanogr. 29: 805–815.

Noel, D. S. et al. 1986. Effects of forest clearcutting in New England on stream macroinvertebrates and periphyton. – Environ. Manage. 10: 661–670.

Peckarsky, B. L. 1980. Predator–prey interactions between stoneflies and mayflies: behavioral observations. – Ecology 61: 932–943.

Ploskey, G. R. and Brown, A. V. 1980. Downstream drift of the mayfly *Baetis flavistriga* as a passive phenomenon. – Am. Midl. Nat. 104: 405–409.

Power, M. E. 1983. Grazing responses of tropical freshwater fishes to different scales of variation in their food. – Environ. Biol. of Fish. 9: 103–115.

Power, M. E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. – J. Anim. Ecol. 53: 357–374.

Walton Jr, O. E. 1980. Invertebrate drift from predator–prey associations. – Ecology 61: 1486–1497.

Waters, T. F. 1972. The drift of stream insects. – Annu. Rev. Entomol. 17: 253–272.

Wootton, J. T. and Power, M. E. 1993. Productivity, consumers and the structure of a river food chain. – Proc. Natl Acad. Sci. USA 90: 1384–1387.

Supplementary material (available online as Appendix oik-00319 at < www.oikosoffice.lu.se/appendix >). Appendix 1, 2.