

The effects of substrate, predators, and variations in flow on the drift of a lotic *Heptageniidae* mayfly.

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Abstract

Stream conditions have undergone and are likely to continue to experience drastic changes as a result of human-induced climate change and manmade dams. These conditions can have an enormous impact on benthic macroinvertebrates, which are an essential component of stream ecosystems. Drifting is the main method of movement between habitat patches for many macroinvertebrates, including mayflies. In this experiment, I studied the effect of an abrupt increase in flow, different stream substrates, and presence of predators on drift rates of the *Heptageniidae* mayfly from artificial stream channels.

I found that substrate and predators have a significant effect on drift, with more insects drifting from sand than gravel, as well as more from no predators than predators. An increase in flow rate did not change drift rate relative to a flow rate that remained constant. There was a significant interaction effect between sand and absence of predators, with sand substrate increasing drift rates from streams with no predators.

Introduction

Since the Industrial Revolution, humans have been greatly changing the composition of the atmosphere by emitting increasingly large amounts of greenhouse gases and aerosols, both of which are affecting global climate and precipitation patterns. Among these changes is an increase in precipitation extremes, defined as most intense 10% of precipitation events (Russo and Sterl 2010, Shiu et al. 2011). This increase began during the 20th century (Kunkel et al. 1998) and is projected by several different models to continue in the 21st century (Milly et al. 2001, Burke et al. 2005).

As a result of this increased precipitation, floods, which are a natural and important part of river ecosystems, are happening much more frequently than in the past (Groisman et al. 2000, Novotny and Stefan 2006). Organisms have evolved adaptations to survive and sometimes take advantage of floods, but this has occurred over evolutionary time scales, and environmental changes are happening much faster than that (Lytle and Poff 2002).

Humans have also directly altered the physical surface of the earth by constructing dams on most rivers; Lytle and Poff (2002) found that 98% of rivers in the U.S. have been dammed.

These have enormous ecological consequences, as the installation of dams decreases flow rates and changes the path and substrate of rivers, especially upstream of the structure (Stanley and Doyle 2002). Many dams are being removed as part of attempts to restore rivers to their unaltered states (Tullos et al. 2013), but this has ecological consequences as well. Dam removal alters the flow rate of rivers as water is allowed to flow unimpeded, and the substrate of the river changes due to erosion at the former site of the dam and deposition of sediments downstream (Hansen and Hayes 2011, Stanley and Doyle 2002).

Stream biota are greatly affected by these changes occurring in the atmosphere and hydrosphere. As dam removal and other disturbances benefit some species and hurt others, relative macroinvertebrate densities are likely to change. Because macroinvertebrates are an important food source for fishes and are thus vital to energy flow and nutrient cycling in benthic ecosystems (Wills et al. 2005), this will affect the entire ecosystem.

Drift is the main method of transport for macroinvertebrates. They have been shown to drift both passively, when high flow events shear animals from the substrate or the substrate shifts and dislodges the organisms, as well as actively, in search of food, different substrate and flow conditions, and to escape predators (Oldmeadow et al. 2008, Brittain and Eikeland 1987, and Holomuzki 1995). This drift can be greatly dependent on the river's flow regime. In dammed rivers, relative macroinvertebrate densities downstream of the dam have been shown to be affected by daily peak fluctuations in flow (Castro et al. 2012), and macroinvertebrate densities declined after an experimental increase in flow (Irvine 1984). Holomuzki (1995), Winterton (1994), and Kerans et al. (1994) found that the presence of predators had little effect on drift of mayflies in particular, while a review conducted by Wooster and Sih (1994) showed that invertebrate predators have a large effect on the density and drift of macroinvertebrates as a functional group.

Many studies have considered the effects of changing flow, presence of predators, and different substrates on macroinvertebrate drifting and density. However, few of these studies have combined all three of these variables or used an artificial channel setup to maximize their ability to control other variables. This experiment seeks to address these questions as well as contribute to the broader understanding of benthic community structure and dynamics. In the experiment, I ask:

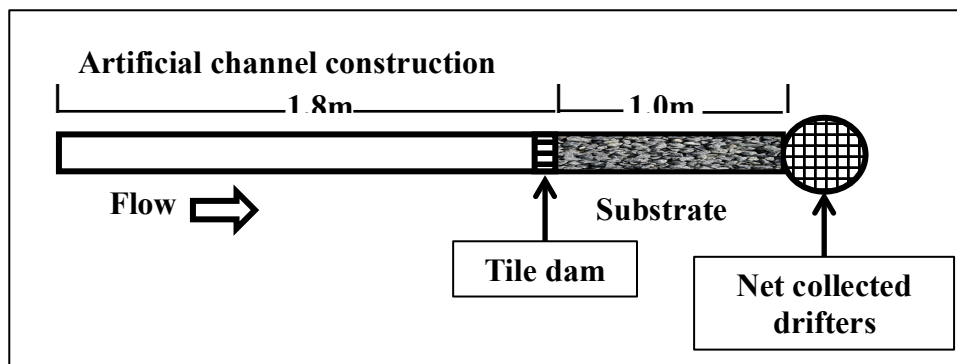
1. Which stream conditions do mayflies prefer? (sand vs. cobble and gravel, presence vs. absence of predators, and constant vs. fluctuating flow)
2. What is the interaction between these 3 variables, i.e. do mayflies show a stronger preference for one stream condition when it is combined with another?

Materials and Methods

The experiment was conducted at the University of Michigan Biological Station Artificial Stream Facility on the East Branch of the Maple River in Emmett County, Michigan, 49769.

Mayflies and stoneflies were collected from various locations on the river using dip nets and kick nets by walking backward upstream and disturbing the substrate; any debris and organisms kicked up were caught in the nets. They were then randomly sorted into groups of ten (mayflies) and two (stoneflies).

Channel construction was based on the experimental set-up from Joe Holomuzki's (1995) experiment conducted at the UMBS Stream Facility. Vinyl rain gutters (2.8 m long, 0.1 m wide, 7 cm high) were used as artificial stream channels. Water was pumped from the Maple River by



a Monarch® pump with 2.54 cm holes and filtered to remove sediment and organisms, then into a plastic

barrel with 8 valves (“head tank”) that each emptied into a channel and regulated flow. Water in each channel flowed through a “pool” created by a dam constructed of four clay tiles (4 x 3 cm) stacked 2 tiles high that collected incoming FPOM (free particulate organic matter), then through a meter-long section containing substrate and insects. Drifting mayflies were captured by a 5.08-cm section of PVC pipe with a piece of window screen glued to one end and attached to each gutter with a short section of K-mart® brand knee-high nylons. Discharge (120 ± 10 mL/s, with an additional 60 ± 10 mL/s for the increased flow treatments, based on USGS measurements of average flow fluctuations for nearby streams) was uniform among all streams. Conductivity,

dissolved oxygen, pH, and temperature were measured in the river and in each head tank to ensure uniformity.

For the four high flow treatments, an extra head tank filled by a sump pump that was connected to a timer was turned on later in the trial. For the treatments containing predators, 2 stoneflies were added to each channel at the same time as the increase in flow. Substrate (sand, gravel, and cobble) was collected from the Maple River and placed in the last meter of each channel. Sand and gravel were spread out to make a smooth layer approximately 1 cm deep, and 6 pieces of cobble measuring approximately one-third to one-half the width of the channel (0.03-0.05m) were placed on top of the gravel in an alternating pattern the length of the substrate.

Mayflies were poured gently into each channel from a Solo® brand plastic cup behind a handheld clay tile (5 x 5 cm) that served as a dam to allow the mayflies to settle and was removed once the mayflies were added. They were placed in the stream at sunset and collected and counted the next morning, then sorted based on treatment and whether they drifted and preserved in 80% ethanol. Stoneflies were added in the same manner, but were reused between treatments.

Drift rate for each treatment was calculated as the number of mayflies that drifted from each channel divided by the number added to the channel (10). Drift rates were compared between treatments and the interaction effect between treatments was calculated using SPSS to conduct an ANOVA analysis.

Results

Substrate, presence of predator, and fluctuating flow effect on drift rate

Heptageniidae drift rates were significantly affected by channel substrate (Fig. 1), and were more likely to drift on sand than gravel/cobble ($F_{1,7} = 19.686$, $p < 0.001$). An absence of predators (Fig. 1) significantly increased drift rate ($F_{1,7} = 6.354$, $p = 0.013$). We saw no correlation between drift rate and a 50% increase in flow ($F_{1,7} = 0.223$, $p = 0.638$) (Fig. 1) during each trial. Stonefly drift rate from the channels was unaffected by substrate or flow, and mayfly drift was not affected by stonefly drift (F , p). Sand substrate also significantly increased the size of the presence of predator effect ($F_{1,7} = 3.98$, $p = 0.050$) (Fig.2).

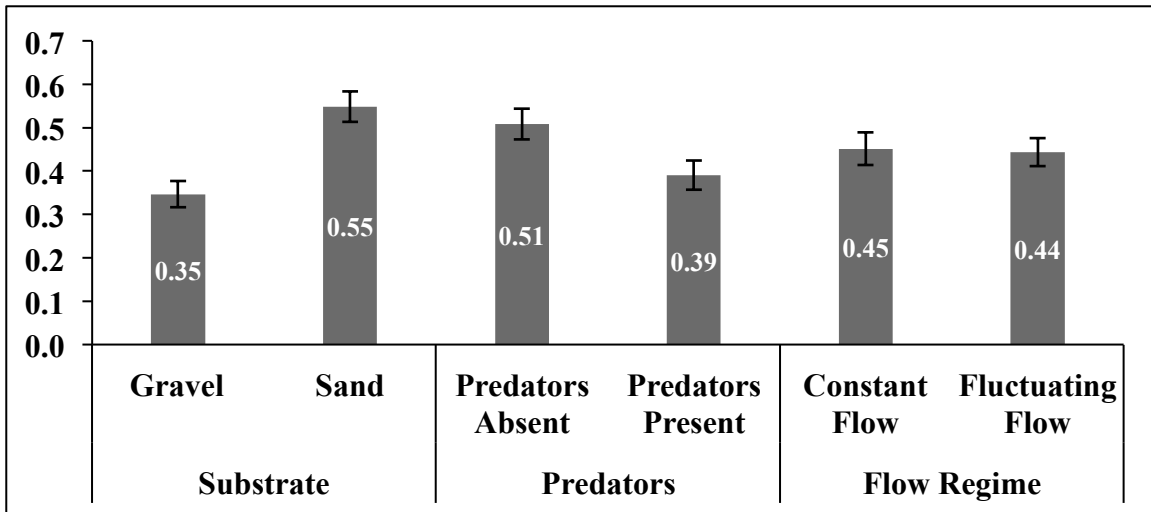


Fig. 1. Mean drift rate (+1 SE) from various substrates, predator conditions, and flow regimes in artificial stream channels.

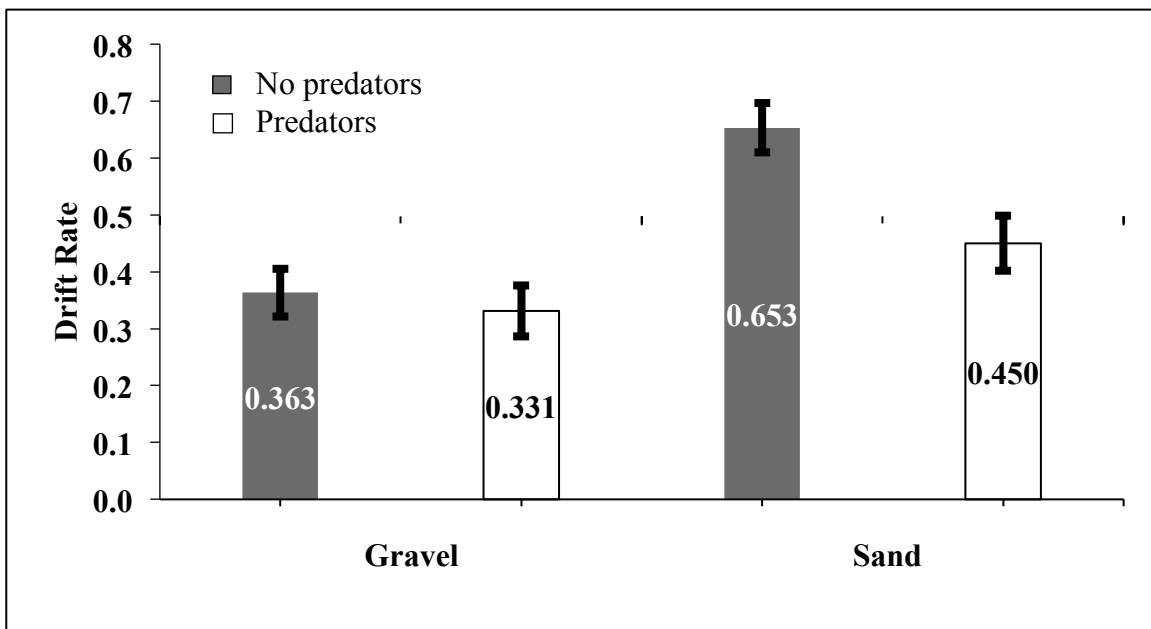


Fig. 2. Mean drift rate (+1 SE) from different predator and substrate combinations in artificial stream channels.

Discussion

Sand substrate and absence of predators both significantly increased mayfly drift rate, while fluctuating flow had no effect on drift rate. There was a significant interaction effect between substrate and predator absence.

More insects drifted from streams with sand substrate than with gravel and cobble. This supports the findings of several studies (Holomuzki 1995, Fairchild and Holomuzki 2004, Gibbins et al. 2009). Sand is a less stable substrate than gravel, so insects are more vulnerable to passive drift when they are dislodged by shifting substrate (Holomuzki 1995). It also provides less shelter than gravel and cobble from shearing forces (Hoover and Ackerman 2003), which may be another cause of passive drifting. This supports evidence that some macroinvertebrates prefer grooves and cracks in artificial substrate to flat surfaces (Fairchild and Holomuzki) as well as bottom surfaces of rocks (Kohler 1982). One study found that while sandy stretches did not significantly affect macroinvertebrates' ability to drift through those sections of the river, they did impede their upstream movement, even under low flow conditions (Luedtke and Brusven 1975), which indicates that sand is a difficult substrate for macroinvertebrates to cling on to and that the higher drift rates that we observed may be passive, rather than active. However, while this experiment clearly shows that mayflies tend to drift more from sand, it is impossible to tell from our results whether it is active or passive.

Contrary to our hypothesis that predators create a less hospitable environment for mayflies and thus increase drift rate, significantly more insects drifted from streams that lacked predators. This is contrary to the results of many studies that found that because Order *Ephemeroptera* (mayflies) is one of stoneflies' preferred prey groups (Siegfried and Knight 1975), the presence of stonefly and other invertebrate predators will decrease mayfly density (Peckarsky et al. 1989, Peckarsky et al. 2007) and increase drift rates (Kerans et al. 1994, Oldmeadow et al. 2008). However, many of these studied the drift of many different invertebrates, both specific taxa and macroinvertebrates as a broader group. The family of mayflies studied here, *Heptageniidae*, prefers to crawl, rather than drift, to avoid predators (Peckarsky 1979), whereas many of the taxa discussed in other papers, such as the mayfly families *Baetidae* and *Ephemerellidae*, preferred to swim or adopt a defensive posture to avoid predators. *Heptageniidae* experience the lowest mortality when crawling to escape predators as opposed to posturing or swimming and drifting away (Corkum and Clifford 1979, Peckarsky 1995).

A mid-trial increase in flow (50% increase) did not appear to affect mayfly drift. This is inconsistent with other studies that found that floods (Brittain and Eikeland 1987, Céréghino et al. 2003) and less catastrophic increases in flow (Poff and Ward 1990, Imbert and Perry 1999)

both increase drift. Further, we found no interaction between substrate and flow variation, which is inconsistent with Brittain and Eikeland's finding that drift as a result of floods was much higher from gravel substrate than sand. However, these results were based on a much larger change in flow than in our artificial streams: flow in our streams was raised by a factor of 0.5, whereas others studied the effect of flow increased by factors of 2.5-3 (Imbert and Perry), 2, 5, and 11 (Cereghino et al). The amplitude of the increase was shown to be more important than the peak value, indicating that the changes studied in this experiment may not have been of sufficient magnitude to show an effect, either by shearing insects from the substrate or creating an environment that results in active drift.

There was a significant interaction effect between substrate and absence of predators, with sand strengthening mayfly's tendency to drift more often with predators absent. Many studies have found that predators have a behavioral effect on prey: there is often a tradeoff between optimal habitat or resource acquisition and reducing the risk of predation (Grubb and Greenwald 1981, Lima and Dill 1989, Poff et al. 1990, Pomeroy 2005). In this case, the mayflies appear to forego the opportunity to move on to a patch with their preferred substrate in favor of more easily evading predators and avoiding consumption.

The results of this experiment indicate that the movement of sediment (or lack thereof) that comes with dams and their removal, floods, and droughts could lead to macroinvertebrate emigration, which would be detrimental to the riverine ecosystem. As stream conditions inevitably change as a result of anthropogenic carbon emissions and dam construction and removal, an understanding of aquatic community dynamics will be increasingly important. Since benthic macroinvertebrates are an essential component of nutrient cycling and energy flow in those communities, an understanding of the effects of changing conditions on macroinvertebrates will be vital to understanding how the ecosystem as a whole will be affected.

Though algae growth was removed from the channels prior to each trial, food availability was not taken into account as a driver of drift in this experiment, nor was the possible effect of consumption by the stonefly predators, nor the potential indirect effects of flow on food availability and dissolved oxygen. Due to the number of mayflies necessary for each trial, it was impossible to collect them all at the same time, so the time spent in an artificial stream-side holding chamber was not consistent across all subjects. This paper was constrained to only two treatments for each variable studied, so further experiments could study the influence of

vertebrate predators as well as invertebrate, different substrates in addition to sand and gravel, and a wider range of flow treatments. Replication of the experiment with multiple taxa— other mayfly and other macroinvertebrates would provide valuable insight into whether this experiment has implications for *Heptageniidae* alone or if it is generalizable for all macroinvertebrates.

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