Deleterious effects of net clogging on the quantification of stream drift

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0365.R2
Manuscript Type:	Article
Date Submitted by the Author:	17-Nov-2016
Complete List of Authors:	Muehlbauer, Jeffrey D.; U.S Geological Survey, Grand Canyon Monitoring and Research Center Kennedy, Theodore A.; USGS, Grand Canyon Monitoring and Research Center Copp, Adam J.; USGS, Grand Canyon Monitoring and Research Center Sabol, Thomas A.; U.S Geological Survey, Grand Canyon Monitoring and Research Center
Keyword:	DRIFT < General, STREAMS < Environment/Habitat, RIVERS < Environment/Habitat, METHODOLOGY < General, ECOLOGY < General
Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.	
Supplement 1.MP4	

SCHOLARONE™
Manuscripts

1 **Deleterious effects of net clogging on the quantification of stream drift**

2 **Jeffrey D. Muehlbauer, Theodore A. Kennedy, Adam J. Copp, and Thomas A. Sabol**

3 US Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and
4 Research Center, 2255 N. Gemini Drive, Flagstaff, Arizona, 86001, USA

5 emails: jmuehlbauer@usgs.gov, tkennedy@usgs.gov, adamcopp2@gmail.com, tsabol@usgs.gov

6 ***Corresponding author:*** Jeffrey D. Muehlbauer (phone: +1 928-556-7328, fax: +1 928-556-7100,
7 email: jmuehlbauer@usgs.gov)

Draft

Abstract:

Drift studies are central to stream and river ecological research. However, a fundamental aspect of quantifying drift—how net clogging affects the accuracy of results—has been widely ignored. Utilizing approaches from plankton and suspended sediment studies in oceanography and hydrology, we examined the rate and dynamics of net clogging across a range of conditions. We found that nets clog non-linearly over time, and that suspended solid concentrations and net mesh size exerted a strong effect on clogging rates. Critically, net clogging introduced unpredictable biases in resultant data due to the inaccuracies in water volume estimates introduced by progressive clogging. This renders the widespread approach to linearly “correct” for clogging inadequate. Using a meta-analysis of 77 drift studies spanning 25 years, we demonstrate that the detrimental effects of net clogging are routinely unappreciated, even though the results of most of these studies were likely affected by clogging. We close by describing an approach for avoiding net clogging, which will increase the accuracy and reproducibility of results in future freshwater, lotic drift studies.

22 Introduction

23 Drift in stream and river ecosystems is essential to the maintenance, dispersal, and life
24 histories of many freshwater invertebrate populations and also provides a key food source for
25 drift-feeding fishes (Brittain and Eikeland 1988; Naman et al. 2016). As such, stream drift is
26 often used as a metric for assessing invertebrate community composition or density across sites
27 and as an indicator of food availability to fish populations (Allan and Russek 1985; Rader 1997;
28 Malmqvist 2002). Bioenergetics and drift foraging models are also increasingly used to
29 understand drivers of fish population dynamics, and these models require high quality drift data
30 as an input parameter (Rosenfeld et al. 2014; Dodrill et al. 2016). Additionally, quantifying drift
31 concentrations or rates is useful for understanding the behavior of individual species in relation
32 to environmental perturbations and the presence or absence of predators (Wallace and Hynes
33 1981; McIntosh et al. 2002; Bruno et al. 2013). Although the approach to quantifying drift for
34 these diverse objectives is varied, drift measurements are rooted in some unit of water flux
35 (Smock 2006); thus, obtaining high quality results from any drift measurement requires an
36 accurate estimation of water volume sampled.

37 The importance of accurately quantifying the volume of water sampled is not limited to
38 studies of drifting stream invertebrates and organic matter: it has long been recognized by
39 researchers studying plankton in oceans and lakes and by those investigating suspended sediment
40 concentrations in streams and rivers (Kofoid 1897; Federal Interagency Sedimentation Project
41 1941). In these fields, data quality is assessed using either net filtration or sampler intake
42 efficiency for plankton and suspended sediment studies, respectively (Smith et al. 1968; Sabol
43 and Topping 2013). In plankton studies specifically, the filtration efficiency (FE) of a net serves
44 as a proxy for the extent to which a net is clogged: under perfect conditions, FE is 100% and

flow moves unimpeded through the net. The plankton literature seems to have converged upon 85% FE (i.e., the velocity in the net is 85% the value outside of it), as an acceptable benchmark for maintaining high quality data collection (Tranter and Smith 1968), and a common focus of these studies is designing sampling equipment and methods that demonstrably minimize reductions in FE (Smith et al. 1968). In fact, although they are rarely cited within the stream ecology literature (but see Tilley 1989), several of the methodological issues raised and advancements made in these fields are directly transferable to the study of lotic, freshwater drift. For example, plankton net design experiments have identified ideal mesh open area ratios and mouth characteristics that will not restrict flow (Tranter and Smith 1968). Similarly, other experiments have investigated appropriate net mesh sizes for promoting high levels of water filtration (Slack et al. 1991; Mack et al. 2012), and have assessed sample repeatability and precision when different sampling methods and equipment are used (Sabot and Topping 2013).

In spite of its fundamental effect on drift concentrations and the attention it has garnered in related aquatic fields, explicit quantification of FE is almost entirely absent from the stream ecology drift literature (Faulkner and Copp 2001). Nonetheless, researchers have recognized for decades that nets clog and that this may affect calculated drift results (Waters 1969). For example, in a classic paper, Allan and Russek (1985) mathematically account for the effect of clogged mesh on water velocities moving through the net by taking velocity measurements at the beginning and end of sample and averaging these values. This approach, which has been cited frequently by subsequent researchers (Matthaei et al. 1998), fits a two-point linear regression to the in-net velocity vs. time curve, thus implicitly assuming that clogging occurs linearly over the course of sample collection. However, continuous velocity data from oceanic plankton research and at least one stream drift study suggest that net water velocity declines non-linearly with

progressive clogging (Tranter and Smith 1968; Walne et al. 1998; Faulkner and Copp 2001). Results will thus be biased when fitting a linear regression to data that are more exponential or logistic in nature. Such biases are non-trivial: in one recent assessment of suspended sediment collection methods, the error in concentration estimates arising from decreases in water intake efficiency into samplers was routinely > 50% (Sabol and Topping 2013). Thus, the quality and repeatability of stream and river drift research may be improved markedly by adopting methods that explicitly account for the deleterious effects of clogging.

In this study, we explored the dynamics of drift net clogging and its effects on resultant drift data. Specifically, we assessed the extent to which sample duration, mesh size, and suspended solid concentrations affect the functional response and timing of net clogging. We also carried out a meta-analysis to put our field results in the broader context of drift studies in streams and rivers, and to assess the extent to which past researchers have addressed net clogging or attempted to compensate for its effects. We close by describing an approach to drift sampling that will minimize the effects of clogging and maximize reproducibility across freshwater drift studies.

Materials and methods

Field sampling sites

Drift sampling was carried out on five dates in 2014, in three streams and rivers in Arizona, USA that encompassed a broad range of conditions (Table 1¹). We collected eight samples on the Colorado River at Lees Ferry (36.864808°, -111.587786°) to assess the effects of sample duration on clogging rates. Additionally, we collected two samples on the Colorado River near Horseshoe Bend, 15 km upstream of Lees Ferry (36.885689°, -111.522999°), to compare and contrast clogging dynamics for two common mesh sizes (250 and 500 µm). The

Colorado River at both sampling locations is ~ 100 m wide and 5 m deep. Flow is highly regulated by Glen Canyon Dam ~ 25 km upstream of Lees Ferry, and the river is relatively clear and cold (mean 11 °C), with highly variable daily discharge (mean 354 m³ s⁻²) and a depauperate invertebrate fauna dominated by aquatic Diptera and non-insects, including non-native *Gammarus lacustris* amphipods and *Potamopyrgus antipodarum* mud snails (Kennedy et al. 2014; Kennedy et al. 2016). Both sites are devoid of canopy cover and in-stream primary production was relatively high during sample duration experiments in spring (T.A. Kennedy unpublished).

Additional sample duration experiments were conducted in the fall on the unregulated Wet Beaver Creek (34.670111°, -111.712427°) and on the Salt River ~ 650 m downstream of Stewart Mountain Dam (33.559424°, -111.533374°), both in central Arizona (Table 1). In contrast to the Colorado River, flow conditions in these systems are more typical of the streams for which drift methods are particularly well described (Smock 2006), with channel widths ~ 10–30 m and depths ~ 1–1.5 m, respectively. The invertebrate community of Wet Beaver Creek is also notably more diverse than the Colorado River sites (LeRoy and Marks 2006). Wet Beaver Creek has dense canopy cover, but sampling occurred prior to onset of substantial leaf litter infall. Sampling on the Salt River, however, appeared to be coincident with a period of high seasonal sloughing of algae (A.J. Copp, personal observation; Supplements 1, 2²).

Drift sampling

Drift samples were collected to assess either (1) the dynamics of net clogging with increasing sample duration, or (2) the effects of net mesh size on clogging. Of the 19 drift samples collected, 17 were used to address the first objective, while 2 addressed the second (Table 1). For the sample duration tests, 4–5 net deployments (i.e., samples) were carried out for

114 a given site and sample date, ranging in duration from 8 min to 4 h. This yielded a dataset
115 containing four discrete sample sets, with each set representing a suite of sample durations across
116 a range of probable levels of net clogging. Nets were deployed in succession at the same location
117 in the river, rather than concurrently across a cross section, to avoid potential biases arising from
118 sampling drift at different locations within a channel. Additionally, samples within a set were
119 collected in succession, in random order.

120 Drift nets and sampling methods were chosen so as to be appropriate for the stream order
121 being sampled. A 2.5-m long, 250- μ m mesh, conical plankton net with a 0.5-m diameter, bridled,
122 circular opening was used for the sample duration sets collected at the Lees Ferry site on the
123 Colorado River (Table 1). The net was deployed mid-channel using a hand-powered winch (A-
124 reel, Rickly Hydrological Company, Columbus, Ohio, USA), off the front of a moored boat
125 (Kennedy et al. 2014). A 40-kg lead sounding weight was attached to a 1-m long stainless steel
126 chain at the end of the winch cable to prevent the net from being swept downstream by the
127 current, and the net was attached halfway (0.5 m) down this chain.

128 For sample duration experiments on the Salt River and Wet Beaver Creek (Table 1), a
129 0.9-m long, rectangular net with 250- μ m mesh and a 0.44 x 0.25-m opening was used for
130 sampling. The net was completely submerged mid-channel and held in place using rebar posts.
131 This net design and sampling strategy is widely used in drift studies (Smock 2006). Similar
132 methods were used for the net mesh size experiment, which occurred at wading depth near the
133 banks of the Horseshoe Bend site on the Colorado River. Two nets were deployed at this site:
134 one each with 250 and 500- μ m mesh, but they were otherwise identical to those used on the Salt
135 River and Wet Beaver Creek.

Filtration efficiency measurement

The extent of net clogging was assessed quantitatively using measurements of instantaneous filtration efficiency (FE_{inst}), which indicate the extent to which flow through the net at a given time is representative of ambient (out-of-net) flow conditions in realtime and is calculated as follows:

$$(1) \quad FE_{inst} = \frac{V_{net}}{V_{amb}} \times 100\%$$

where V_{net} is the velocity of water flowing in the net and V_{amb} is the ambient velocity of water outside the net. Initial and final FE_{inst} values were also calculated as the average FE_{inst} for the first or last 30 seconds of sample collection; these were used in comparing the magnitude of change in FE_{inst} due to net clogging over a sample's duration. For a theoretical, perfect drift sample, velocity within the net is identical to ambient velocity, and $FE_{inst} = 100\%$ and remains so throughout the sample duration; in suboptimal conditions, $FE_{inst} < 100\%$ and may even approach 0% as nets become completely clogged (Tranter and Smith 1968). To describe how nets clog over time mathematically, three candidate decay functions—linear, exponential, and logistic—were fit to the FE_{inst} vs. time data, and their goodness of fit was compared using AIC. These and all subsequent analyses were carried out using R statistical software (R Core Team 2015).

To measure FE_{inst} , we set up two electronic flowmeters (General Oceanics model 2031H, Miami, Florida, USA). The first was mounted within the mouth of the net to record velocity into the net, while the second was installed adjacent to the net, 0.3–0.7 m away, to record ambient flow velocity. Pilot experiments indicated that the two flowmeters were sufficiently close that they both experienced similar streamflow conditions, yet far enough away that the adjacency of the net did not affect ambient velocity readings (A.J. Copp, unpublished). In addition to

recording water velocity, these flowmeters provided a record of the total distances of water (d) that passed by them, allowing us to calculate an overall, average FE (FE_{avg}) for each sample as follows:

(2)
$$FE_{avg} = \frac{d_{net}}{d_{amb}} \times 100\%$$

Estimating suspended solids concentrations

The concentration of total suspended solids (TSS) was calculated for each of the four sample sets (Table 1), representing a range of probable FE_{avg} values. TSS encompasses the bulk mass of organic matter, invertebrates, and sediment particles larger than the net mesh size and is analogous to drift concentration (often erroneously referred to as “drift density”; Allan and Russek 1985). Germane to the broader field of drift research, TSS also can serve as a proxy for the relative concentration of individual components of the drift, such as invertebrates that are the foci of many studies (Smock 2006).

In the field, drift nets were rinsed thoroughly onto a 250- μ m sieve using in-stream dunking, pump sprayers, and squirt bottles. The sample was then transferred to a polyethylene bag, labeled with a barcode (Copp et al. 2014), and kept on ice until their return to the laboratory. In the lab, samples were placed into pre-weighed tins, dried for 48–72 h at 70 °C, depending on sample volume, and weighed to the nearest 0.1 mg on a microbalance.

We computed the TSS for each sample set as follows:

(3)
$$TSS = \frac{M}{A \times d}$$

where M is the collected mass or biomass of a drift sample, A is the area of the net mouth, and d is the distance of water sampled by the net as described in Eq. 2. For a given sample, TSS values could be computed based either on ambient or net flowmeter data (d_{amb} or d_{net} , Eq. 3). These two TSS values should be equivalent when conditions for a given sample are perfect (100% FE_{avg}). Thus, the deviation from unity between ambient and net-mounted flowmeter values (TSS_{amb} and TSS_{net} , respectively) indicates the degree to which clogging is affecting a given drift concentration value. To assess the effects of net clogging on TSS, we first determined an expected TSS (TSS_{exp}) for each sample set, representing the TSS under optimal, unclogged conditions. We computed TSS_{exp} as the average of the TSS_{net} and TSS_{amb} values from the shortest sample within each sample set. We chose the shortest samples because these nets were minimally clogged, with FE_{avg} nearest 100%, and were likely the most representative of the true TSS. We then calculated the deviation from TSS_{exp} for each sample as follows:

$$(4) \quad \text{Deviation} = \frac{|TSS_{\text{net}} - TSS_{\text{exp}}| + |TSS_{\text{amb}} - TSS_{\text{exp}}|}{2 \times TSS_{\text{exp}}}$$

Meta-analysis

To assess how sample times vary across drift studies, we conducted a meta-analysis of drift literature published from 1990 to 2014 by searching for the term “*invertebrate drift” in Web of Science. Because our research questions were specific to stream and rivers, we limited the search to five journals with a heavy focus on lotic ecosystems: *Freshwater Biology*, *Hydrobiologia*, *Canadian Journal of Fisheries and Aquatic Sciences*, *Journal of the North American Benthological Society*, and *Archiv für Hydrobiologie*. This yielded 209 studies, of which 77 described their drift sampling characteristics with enough detail to be included in the

meta-analysis. These characteristics included not only sample duration, but also the velocity and volume estimation methods used (continuous measurements or measurements at the beginning, end, or beginning and end of sample collection), net or sampler structural characteristics (mesh size, mouth shape and area, and net length), and whether clogging was explicitly mentioned in the study¹. To determine whether certain net characteristics might influence researchers' decisions about how long to deploy drift nets (e.g. longer nets might clog more slowly and thus be deployed for longer than shorter nets), the relation of these variables to sample duration was compared using individual linear regressions.

Results

Total and instantaneous filtration efficiencies

Across the 19 field drift samples, FE_{inst} decreased in 18 nets over the sample duration (Table 1, Fig. 1). The single exception was a Colorado River sample taken at low discharge that remained at ~ 100% FE_{inst} throughout the short, 15 min duration of the sample. Initial FE_{inst} was ~ 100% for all samples, with the exception of the five on the Salt River that had an average initial FE_{inst} of 77%. For the four sample sets representing nets deployed for different durations at the same site on the same date (17 total samples), both FE_{avg} and the final FE_{inst} values declined within each sample set as sample duration increased (Table 1). Based on regression models, the mean sample duration at which FE_{inst} dropped below 85% was 27 min for Colorado River sample sets and 43 min for Wet Beaver Creek. On the Salt River, FE_{inst} was < 85% even at the onset of sampling for all five samples.

The remaining two samples that were not grouped in sample sets consisted of a side-by-side comparison of 250 and 500- μ m net mesh sizes on the Colorado River. Between these, the 500- μ m net had a higher FE_{avg} and final FE_{inst} after a 3-h duration than the 250- μ m net after only

2 h of sample collection (Table 1). For direct comparison, FE_{avg} and FE_{inst} of the 500- μ m net were 72% and 29% after 2 h, respectively. These values are 1.5–1.8 times higher than the respective values from 2-h sample collected with a 250- μ m net. Similarly, the time at which the 250- μ m net dropped below 85% FE_{inst} was 17 min, whereas it took 42 min for the 500- μ m net to reach this clogging benchmark.

Instantaneous filtration efficiency curve fitting

In modeling the relationship between FE_{inst} and time, the logistic curve was the most strongly supported function in 12 of 19 samples (Table 1). These included all of the Colorado River samples, as well as the 2 and 4-h samples on Wet Beaver Creek (Fig. 1). The linear and logistic functions were equally supported for the 15-min sample on the Salt River, which was the only sample within that sample set where a logistic curve could be fit. Otherwise, the linear curve was the most strongly supported model outright in three of the remaining Salt River samples (0.5, 1, and 2 h), and was received equal support with the exponential curve for the fourth (the 8-min sample). The exponential curve was the most strongly supported model only for the two longest samples (2 and 4 h) on Beaver Creek.

Effect of suspended solids on instantaneous filtration efficiency

Filtration efficiency of nets was inversely related to TSS. For an initial period of ~ 30 min, FE_{inst} was similar for most sample sets (excepting the Salt River), with values ~ 100% (Fig. 2). But after this initial period, FE_{inst} was highest for those sample sets where TSS was lowest, and remained so throughout the sample duration until nets were effectively fully clogged ($FE < 20\%$). Further, FE_{inst} decreased more rapidly for sample sets with higher TSS. Wet Beaver Creek, which had the lowest TSS, had higher FE_{inst} values than at other sites. The Salt River, with TSS 3–10 times greater than other sites, had markedly lower FE_{inst} values than other sample

sets from the onset of sample collection. Both Colorado River sets, with TSS between those of Wet Beaver Creek and the Salt River, also had middling FE_{inst} values throughout the majority of their sample durations.

Because net clogging should affect velocities within the net but not ambient water velocity out of the net, values of TSS derived from these two flowmeters should deviate more from one another with decreased FE_{avg} and increasing levels of net clogging. Across the 17 samples that comprised the four sample sets, these deviations were indeed small when FE_{avg} was near 100% (Fig. 3). Percent deviation was also strongly, inverse-linearly related to FE_{avg} . Thus, as FE_{avg} decreased for increasingly clogged nets, the deviation in TSS values calculated from ambient and net-mounted flowmeters increased proportionally.

Meta-analysis

Our search for published studies yielded 77 papers that described drift sampling characteristics in sufficient detail to be included in the meta-analysis (Table 1, Supplement 3¹). Among these 77 studies, 65% deployed nets for at least 30 min, and more than half (53%) deployed nets for at least 1 h (Fig. 4). Twenty three (30%) of the studies made some mention of clogging in the Methods section of their papers, either in reference to steps taken to avoid clogging or in recognition that clogging may have occurred.

Among studies that specified their velocity measurement methods (56 total), three general approaches were utilized: measuring velocity continuously, at the beginning and end of sample collection, or at the beginning or end of sample collection¹. Six studies (11%) explicitly stated that continuously measured velocity in the net mouth to determine the distance of water passed through the drift net and thus the volume of water filtered by the net over the duration of sample collection. In contrast, 27 studies (48%) measured velocity twice: once each at the

beginning and end of sample collection, and these velocities were averaged to compute water sample volume. Finally, 23 studies (41%) used a velocity measurement from either the beginning or the end of the sample to compute sample volume. For this latter method, velocity measurements were nonetheless commonly taken both at the beginning and end of sample collection—possibly as a check to ensure that entrance velocities did not decrease over the duration of sample collection and that clogging was avoided—but these measurements were not averaged as with the second method. Across studies that explicitly mentioned clogging in the Methods, 19% measured velocity continuously over the course of sample collection, compared to 6% for studies that did not mention clogging.

Among the six drift net study variables included in the meta-analysis, the only one that was significantly related to sample duration was whether clogging was mentioned in the Methods (Table 2). If clogging was not mentioned, nets were deployed for an average of three times longer than if it was mentioned (Table 3). Notably, studies that measured velocity during only the two discrete times at the beginning and the end of the sample also deployed nets an average of 2.1–2.5 times longer than studies that measured velocity continuously or those that only measured velocity once. Regression results indicated that these differences were not significant across the three factor levels, however.

Discussion

On the dynamics of net clogging

Few drift studies in streams and rivers have assessed the dynamics of net clogging. As a consequence, most researchers implicitly assume that clogging happens linearly, as evidenced by the linear methods used to derive the total volume of water filtered over a sample collection (Culp et al. 1994; Matthaei et al. 1998; Miller and Judson 2014). Results from the one study that

explicitly investigated net clogging did find that an inverse exponential curve better described decreases in FE than a negative linear function (Faulkner and Copp 2001). However, that research might best be viewed as an initial exploration on the topic: clogging was not the focal point of the study, which was limited to one river, only compared linear and exponential functions (i.e., a logistic function was not considered), and only utilized velocity measurements at the beginning and end of sample collection.

Our results indicate that the clogging of drift nets tends to occur non-linearly (Table 1, Fig. 1). Specifically, decreases in FE_{inst} and concomitant net clogging generally proceed according to a logistic function. This is broadly consistent with studies from the comparable realm of planktonic drift in oceans, where logistic declines have also been shown (Smith et al. 1968; Walne et al. 1998). The exceptions to this pattern in our field studies may have been a special case: in the Salt River, TSS was 3–10 times higher than at our other sampling sites, apparently due to the timing of sample collection during pronounced, seasonal sloughing of algae (Supplements 1, 2²). At this site, initial FE_{inst} values were already much lower than 100% so it is predictable that a logistic curve, which is partially defined by an initial period with values near an upper asymptote (100% FE_{inst}), should not fit well to such data. Indeed, this result is also consistent with results from planktonic drift in oceans, where apparently logistic curves arise from high-quality samples, while poor-quality samples from more rapidly-clogged nets appear exponential (Smith et al. 1968). Similarly, the remaining samples in our dataset where a logistic curve was not the most strongly supported model were short-duration samples on Wet Beaver Creek. In these samples, TSS was sufficiently low that FE_{inst} remained very high throughout the duration of drift sample collection and did not reach a lower (0% FE_{inst}) asymptote, rendering the logistic function similarly inviable. For longer samples at this site on the same date (and in all

remaining samples across other sites in our dataset), a logistic curve was the most strongly-supported model.

Unfortunately, the non-linear clogging of nets suggests that the common approach of computing average water velocity from measurements only at the beginning and end of drift sample collection introduces substantial error in drift concentration values. Such a “two-measurement approach” essentially fits a straight line to an inherently non-linear FE vs. time curve. The area under this curve is equivalent to the distance of water filtered, which is used in the denominator of the drift concentration equation (d in Eq. 3); thus, errors in this measurement can have a strong effect on consequent drift concentration values. Such estimation issues have been recognized by past researchers (Faulkner and Copp 2001; Smock 2006); however, it has so far been unappreciated that these errors may result in either under or over-estimates of drift concentration, contingent on the inflection point of the logistic function for a given drift sample. Volumes derived from the two-measurement approach therefore cannot be coerced to derive accurate drift net concentrations in any consistent fashion. Indeed, “corrections” to these data based on a two-point line may ultimately be just as problematic as drift concentration data derived from only a single velocity measurement: the latter will at least be reliably an under or over-estimate, depending on whether the velocity measurement occurred at the beginning or the end of sample collection, respectively.

In line with expectations, our samples from net deployments in systems with higher suspended solids concentrations experienced more rapid clogging (Fig. 2). Notably, for our samples on the Salt River where TSS was 3–10 times higher than any other sample set, all experienced clogging from the onset of sampling, as evidenced by initial FE_{inst} values $\sim 70\%$. This suggests that, under certain conditions such as high water velocity and/or high suspended

solid concentrations, there may be no “safe” sample duration for a given net configuration (i.e., within the initial period of the logistic curve where FE_{inst} remains near its 100% asymptote). For researchers working in such conditions, some drift net designs are simply inappropriate. Our Salt River drift nets would have clogged much less rapidly if we had used a net with a smaller net open area ratio (Tranter and Smith 1968) or a coarser, 500- μ m net, for instance, rather than the 250- μ m net used for this and other sample sets. As our results for the two Colorado River samples with these different net mesh sizes demonstrate, the choice of a coarser net can decrease the rate of clogging by a factor of two or more (Table 1). Nonetheless, utilizing a coarser net on the Salt River would have made comparisons with our other sample sets more difficult, and would have also biased the collection of invertebrates and other suspended particles toward larger size classes (Smock 2006). Such issues are difficult to rectify after-the-fact; thus, a priori consideration of clogging when designing drift studies is essential.

Net clogging compromises drift concentrations

Our discussion of FE and net clogging to this point has implicitly raised two tradeoffs that researchers encounter when quantifying drift. These can be expressed formally as follows: 1) researchers may attempt to somehow “correct” for net clogging, or alternatively to deploy drift nets for sufficiently short durations to avoid clogging; and 2) researchers may utilize inappropriate sampling equipment and designs for their study systems and acknowledge that clogging influences their data, or alternatively they may adapt their sampling methodology to avoid clogging and acknowledge that certain taxa may be underrepresented with this method. Our results demonstrate that in both of these cases only the latter option—designing studies to minimize clogging—is viable.

Under severe clogging, conditions in the net cease to be even remotely representative of ambient conditions outside of the net. In our Salt River samples, for example, we observed large organic matter particles being forced around the net mouth, and in some cases even being backflushed out of the net as flow conditions within the net began to reverse, pushing water anachronistically upstream (Supplements 1, 2²). Thus, it is impossible to “correct” for the effects of low FE, and clogging introduces unpredictable bias in samples. The only reliable drift data, therefore, are those that come from an unclogged net with high FE. Such data may be biased if methodological compromises must be made to ensure clogging is minimized (e.g., small taxa such as midges will be under-represented in settings where coarse mesh nets are needed), but these are at least biases that researchers can anticipate and describe, not the unaccountable variety that arise from net clogging.

Meta-analysis

Only 30% of the 77 papers included in the meta-analysis mentioned clogging in their Methods sections, suggesting that many authors are generally unaware of the potential impacts of clogging on their datasets. Further, if researchers are cognizant of the deleterious effects of clogging, they deploy drift nets for dramatically less time (10 min versus 2 h) than would be expected by chance. No other characteristics of net deployment were significantly related to sample duration. This suggests that researchers are generally not making decisions on equipment based on avoiding net clogging, such as would be the case if studies with long-duration samples routinely used longer, coarser mesh nets, for example.

Overall, the mean sample duration of ~ 6 h for studies included in the meta-analysis was substantially longer than any of our field experiments, which ranged from 15 min to 4 h. Nonetheless, for the longest samples in each of our four datasets, the final FE_{inst} was ~ 50% or

less (ranging from 11–54%), indicating that nets were substantially clogged across the range of conditions encompassed by these sample sets. Indeed, our nets were definitively clogged across all four sample sets after 1 h (final FE_{inst} range of 16–78%), which was the median sample duration for studies included in the meta-analysis. It is thus likely that many of the datasets encompassed by the meta-analysis were influenced by biases associated with moderate-to-severely clogged nets.

Recommendations

Our intent here is not to call the results and knowledge gained from past studies into question; such a polemic would be of little use. Further, the breadth of literature on the subject, spanning decades of research, clearly indicates that important insights have been gained by the quantification of stream drift (Müller 1954; Brittain and Eikeland 1988; Naman et al. 2016). Nonetheless, our results do unequivocally demonstrate that clogging can have a major, deleterious influence on the accuracy of drift concentration data, and should be avoided by researchers in the future.

There may be no truly benign amount of net clogging from the perspective of data quality owing to the linear decrease in the reliability of drift concentration values as FE decreases. This is the stance taken by recent isokinetic sediment sampling studies, in which a sample is only considered reliable if the water intake efficiency of the sampler is $1.0 \pm 10\%$ and the error associated with each measurement is recorded (Sabot and Topping 2013). However, in contrast to sediment, the extremely short durations that would be required to maintain 100% FE in biological drift studies is less practical due to behaviors of invertebrates and organic matter that are inherently poorly mixed and non-isokinetic. For example, sampled invertebrates may be swimming with or against the current (non-isokinetic), while others are embedded en masse in

clumps of drifting algae and leaf litter that periodically enter the net (poorly mixed). Thus, a reasonable goal may be to remove nets prior to reaching the tipping point of the logistic FE vs. time, clogging curve, after which the filtration efficiency of nets degrades rapidly (Fig. 1). Previous studies of planktonic drift in oceans have similarly converged upon sample durations that maintain FE > 85% as being safely outside the range of such tipping points and therefore being acceptable (Smith et al. 1968; Tranter and Smith 1968). Our meta-analysis indicated that there were no consistent methods for describing net clogging in the stream and river drift net literature; we thus suggest that adopting this “85% FE approach” from the oceanic plankton literature would be a useful standard.

Using this 85% FE approach, researchers would monitor water velocity both in and outside the net at the onset of collecting the first sample. In the most simplistic case, these measurements could be taken at intervals using a single handheld flowmeter. In this scenario, nets would be removed on or before the time when water velocity in the net was only 85% of the corresponding ambient measurement; that is, when FE_{inst} reaches 85%. However, a more robust approach would be to use continuously recording flowmeters such as those deployed in the field experiments described in this study. In this case, the sample FE_{avg} can be computed, which is less stochastic than single or spot measurements of FE_{inst} . Additionally, this approach allows sample FE to be calculated and monitored at any time over the duration of sample collection. Regardless of the approach taken, from this first sample (potentially even a test case where the collected sample is discarded), an ideal sample duration for the site could be decided upon and used for all remaining nets deployed under similar conditions. As observed in our Salt River field samples where nets were clogged from the outset, some sampling equipment may also be inappropriate under certain field conditions; this monitoring of FE during the initial sample collection would

also indicate if a change in sampling equipment, such as a longer net with a smaller open area ratio or coarser mesh, is required.

Recent, high-profile calls have lamented the lack of reproducibility in scientific studies (McNutt 2014; Baker 2016). These discussions about reproducibility have even extended to the invertebrate drift specifically (Naman et al. 2016). In the stream drift literature, we suggest that differential approaches to account for the effects of clogging may be one way in which results from similar studies can arrive at divergent conclusions (e.g., Naman et al. 2016 and references therein). By adopting a standardized approach to drift sampling that recognizes the possibility of clogging and takes active measures to avoid it, research in stream and river drift will benefit from increased data quality and reproducibility, allowing the results and knowledge gained from drift studies to be more broadly applicable across these lotic ecosystems.

Acknowledgements

The authors thank A. N. Metcalfe and other members of the Grand Canyon Monitoring and Research Center ecology group and logistics staff for fieldwork support during this study. Funding was provided by the U.S. Department of the Interior Bureau of Reclamation's Glen Canyon Dam Adaptive Management Program. Use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Footnotes

¹Data associated with this work are deposited on the US Geological Survey ScienceBase (URL forthcoming).

²Supplementary materials are available with the article through the journal Web site.

References

- Allan, J.D., and Russek, E. 1985. The quantification of stream drift. *Can. J. Fish. Aquat. Sci.* **42**(2): 210–215. doi:10.1139/f85-028.
- Baker, M. 2016. 1,500 scientists lift the lid on reproducibility. *Nature* **533**(7604): 452–454. doi:10.1038/533452a.
- Brittain, J.E., and Eikeland, T.J. 1988. Invertebrate drift—a review. *Hydrobiologia* **166**(1): 77–93. doi:10.1007/BF00017485.
- Bruno, M.C., Siviglia, A., Carolli, M., and Maiolini, B. 2013. Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology* **6**(4): 511–522. doi:10.1002/eco.1275.
- Copp, A.J., Kennedy, T.A., and Muehlbauer, J.D. 2014. Barcodes are a useful tool for labeling and tracking ecological samples. *Bull. Ecol. Soc. Am.* **95**(3): 293–300. doi:10.1890/0012-9623-95.3.293.
- Culp, J.M., Scrimgeour, G.J., and Beers, C.E. 1994. The effect of sample duration on the quantification of stream drift. *Freshwater Biol.* **31**(2): 165–173. doi:10.1111/j.1365-2427.1994.tb00850.x.
- Dodrill, M.J., Yackulic, C.B., Kennedy, T.A., and Hayes, J.W. 2016. Prey size and availability limits maximum size of rainbow trout in a large tailwater: insights from a drift-foraging bioenergetics model. *Can. J. Fish. Aquat. Sci.* **73**(5): 759–772. doi:10.1139/cjfas-2015-0268.
- Faulkner, H., and Copp, G.H. 2001. A model for accurate drift estimation in streams. *Freshwater Biol.* **46**(6): 723–733. doi:10.1046/j.1365-2427.2001.00707.x.

- 470 Federal Interagency Sedimentation Project. 1941. Laboratory investigation of suspended
471 sediment samplers. Measurement and Analysis of Sediment Loads in Streams Report 5,
472 St. Paul U.S. Engineer District Sub-Office, Hydraulic Laboratory, University of Iowa,
473 Iowa City, Iowa. Available from http://water.usgs.gov/fisp/docs/Report_5.pdf [accessed
474 22 July 2016].
- 475 Kennedy, T.A., Yackulic, C.B., Cross, W.F., Grams, P.E., Yard, M.D., and Copp, A.J. 2014. The
476 relation between invertebrate drift and two primary controls, discharge and benthic
477 densities, in a large regulated river. *Freshwater Biol.* **59**(3): 557–572.
478 doi:10.1111/fwb.12285.
- 479 Kennedy, T.A., Muehlbauer, J.D., Yackulic, C.B., Lytle, D.A., Miller, S.W., Dibble, K.L.,
480 Kortenhoeven, E.W., Metcalfe, A.N., and Baxter, C.V. 2016. Flow management for
481 hydropower extirpates aquatic insects, undermining river food webs. *BioScience* **66**(7):
482 561–575. doi:10.1093/biosci/biw059.
- 483 Kofoed, C.A. 1897. On some important sources of error in the plankton method. *Science* **6**(153):
484 829–832. doi:10.1126/science.6.153.829.
- 485 LeRoy, C.J., and Marks, J.C. 2006. Litter quality, stream characteristics and litter diversity
486 influence decomposition rates and macroinvertebrates. *Freshwater Biol.* **51**(4): 605–617.
487 doi:10.1111/j.1365-2427.2006.01512.x.
- 488 Mack, H.R., Conroy, J.D., Blocksom, K.A., Stein, R.A., and Ludsins, S.A. 2012. A comparative
489 analysis of zooplankton field collection and sample enumeration methods. *Limnol.*
490 *Oceanogr.-Meth.* **10**(1): 41–53. doi:10.4319/lom.2012.10.41.
- 491 Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. *Freshwater Biol.* **47**: 679–694.
492 doi:10.1046/j.1365-2427.2002.00895.x.

- 493 Matthaei, C.D., Werthmüller, D., and Frutiger, A. 1998. An update on the quantification of
494 stream drift. *Arch. Hydrobiol.* **143**(1): 1–19. doi:10.1127/archiv-hydrobiol/143/1998/1.
- 495 McIntosh, A.R., Peckarsky, B.L., and Taylor, B.W. 2002. The influence of predatory fish on
496 mayfly drift: extrapolating from experiments to nature. *Freshwater Biol.* **47**(8): 1497–
497 1513. doi:10.1046/j.1365-2427.2002.00889.x.
- 498 McNutt, M. 2014. Reproducibility. *Science* **343**(6168): 229. doi:10.1126/science.1250475.
- 499 Miller, S.W., and Judson, S. 2014. Responses of macroinvertebrate drift, benthic assemblages,
500 and trout foraging to hydropeaking. *Can. J. Fish. Aquat. Sci.* **71**(5): 675–687.
501 doi:10.1139/cjfas-2013-0562.
- 502 Müller, K. 1954. Investigations on the organic drift in North Swedish streams. *Rep. Inst.*
503 *Freshwater Res. Drottningholm* **35**: 133–148.
- 504 Naman, S.M., Rosenfeld, J.S., and Richardson, J.S. 2016. Causes and consequences of
505 invertebrate drift in running waters: from individuals to populations and trophic fluxes.
506 *Can. J. Fish. Aquat. Sci.* **73**(8): 1292–1305. doi:10.1139/cjfas-2015-0363.
- 507 R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for
508 Statistical Computing, Vienna. Available from <http://www.R-project.org>.
- 509 Rader, R.B. 1997. A functional classification of the drift: traits that influence invertebrate
510 availability to salmonids. *Can. J. Fish. Aquat. Sci.* **54**(6): 1211–1234. doi:10.1139/f97-
511 025.
- 512 Rosenfeld, J.S., Bouwes, N., Wall, C.E., and Naman, S.M. 2014. Successes, failures, and
513 opportunities in the practical application of drift-foraging models. *Can. J. Fish. Aquat.*
514 *Sci.* **97**(5): 551–574. doi:10.1007/s10641-013-0195-6.

- 515 Sabol, T.A., and Topping, D.J. 2013. Evaluation of intake efficiencies and associated sediment-
516 concentration errors in US D-77 bag-type and US D-96-type depth-integrating
517 suspended-sediment samplers. Scientific Investigations Report 2012-5208, U.S.
518 Geological Survey, Reston, Virg. doi:10.3133/sir20125208.
- 519 Slack, K.V., Tilley, L.J., and Kennelly, S.S. 1991. Mesh-size effects on drift sample composition
520 as determined with a triple net sampler. *Hydrobiologia* **209**(3): 215–226.
521 doi:10.1007/Bf00015344.
- 522 Smith, P.E., Counts, R.C., and Clutter, R.I. 1968. Changes in filtering efficiency of plankton nets
523 due to clogging under tow. *J. Conseil* **32**(2): 232–248. doi:10.1093/icesjms/32.2.232.
- 524 Smock, L.A. 2006. Macroinvertebrate dispersal. *In* *Methods in Stream Ecology*. Edited by F.R.
525 Hauer and G.A. Lamberti. Academic Press, Burlington, Mass. pp. 465–487.
- 526 Tilley, L.J. 1989. Diel drift of Chironomidae larvae in a pristine Idaho mountain stream.
527 *Hydrobiologia* **174**(2): 133–149. doi:10.1007/Bf00014061.
- 528 Tranter, D.J., and Smith, P.E. 1968. Filtration performance. *In* *Zooplankton Sampling*. Edited by
529 D.J. Tranter. UNESCO, Paris. pp. 27–56.
- 530 Wallace, R.R., and Hynes, H.B.N. 1981. The effect of chemical treatments against blackfly
531 larvae on the fauna of running waters. *In* *Blackflies: The Future for Biological Methods*
532 *in Integrated Control*. Edited by M. Laird. Academic Press, London. pp. 237–258.
- 533 Walne, A.W., Hays, G.C., and Adams, P.R. 1998. Measuring the filtration efficiency of the
534 Continuous Plankton Recorder. *J. Plankton Res.* **20**(10): 1963–1969.
535 doi:10.1093/plankt/20.10.1963.

Muehlbauer et al.

- 536 Waters, T.F. 1969. Invertebrate drift—ecology and significance to stream fishes. *In* Symposium
537 on Salmon and Trout in Streams. *Edited by* T.G. Northcote. H.R. MacMillan Lectures in
538 Fisheries, University of British Columbia, Vancouver, B.C. pp. 121–134.

Draft

539
Table 1. Drift net deployment characteristics for the samples in this study.

Sample Set		River (Site)	Date	Discharge (m ³ *s ⁻²)	Net mouth Shape	Net mesh Area (m ²)	Duration (µm)	Duration (min)	FE _{inst}		FE _{avg}	ΔAIC		
									Initial	End		Linr	Expn	Lgst
1	1	Colorado R. (LF)	2014-05-07	292	Circular	0.20	250	15	0.93	0.90	0.96	36	24	0
2	1	Colorado R. (LF)	2014-05-07	293	Circular	0.20	250	30	0.94	0.42	0.81	973	1591	0
3	1	Colorado R. (LF)	2014-05-07	294	Circular	0.20	250	60	0.95	0.12	0.60	1564	4679	0
4	1	Colorado R. (LF)	2014-05-07	283	Circular	0.20	250	120	0.89	0.24	0.28	1667	3402	0
5	2	Colorado R. (LF)	2014-05-08	212	Circular	0.20	250	15	1.02	1.03	1.03	7	6	0
6	2	Colorado R. (LF)	2014-05-08	225	Circular	0.20	250	30	1.10	0.90	1.02	5	19	0
7	2	Colorado R. (LF)	2014-05-08	167	Circular	0.20	250	60	0.97	0.30	0.79	573	2467	0
8	2	Colorado R. (LF)	2014-05-08	187	Circular	0.20	250	120	1.05	0.09	0.54	1299	3023	0
9	3	Wet Beaver Ck.	2014-09-30	0.23	Rectangular	0.11	250	30	1.14	0.97	0.97	5	0	NA
10	3	Wet Beaver Ck.	2014-09-30	0.23	Rectangular	0.11	250	60	1.05	0.78	0.93	47	0	39
11	3	Wet Beaver Ck.	2014-09-30	0.23	Rectangular	0.11	250	120	1.00	0.37	0.66	14	661	0
12	3	Wet Beaver Ck.	2014-09-30	0.23	Rectangular	0.11	250	240	1.04	0.24	0.54	478	3602	0
13	4	Salt R.	2014-10-02	6.23	Rectangular	0.11	250	8	0.78	0.65	0.57	1	0	NA
14	4	Salt R.	2014-10-02	6.23	Rectangular	0.11	250	15	0.78	0.26	0.37	0	79	0
15	4	Salt R.	2014-10-02	6.23	Rectangular	0.11	250	30	0.77	0.14	0.26	0	64	NA
16	4	Salt R.	2014-10-02	6.23	Rectangular	0.11	250	60	0.81	0.16	0.18	0	139	NA
17	4	Salt R.	2014-10-02	6.23	Rectangular	0.11	250	120	0.72	0.05	0.10	0	69	NA
18	NA	Colorado R. (HB)	2014-10-16	310	Rectangular	0.11	250	120	1.01	0.19	0.40	2774	4742	0
19	NA	Colorado R. (HB)	2014-10-16	310	Rectangular	0.11	500	180	1.00	0.21	0.52	1572	6343	0

540
Note: Colorado River samples were located at either Lees Ferry (LF) or Horseshoe Bend (HB). Initial and end FE_{inst} are
541
the mean instantaneous filtration efficiency from the first and last 30 seconds of sample collection, respectively.
542
FE_{avg} is the total distance of water passed by the net-mounted flowmeter relative to the ambient flowmeter over the
543
duration of a sample. ΔAICs are for linear (Linr), exponential (Expn), and logistic (Lgst) curves fit to FE vs time

544 data over the duration of each sample. The most strongly supported curve (lowest AIC) for each sample is
545 highlighted in bold.

Draft

546 **Table 2.** Meta-analysis results for the effect of drift study attributes on sample durations.

	<i>f statistic</i>	<i>P value</i>
Net mesh size	0.0983	0.7547
Net mouth shape	0.0004	0.9836
Net mouth area	0.0103	0.9195
Net length	2.6800	0.1093
Clogging mentioned in Methods	4.4510	0.0382
Velocity measurement method	1.9542	0.1517

547 **Note:** Statistics are based upon linear regression. Significant effects are shown in bold.

Draft

548 **Table 3.** Summary sample duration statistics for the studies included in the meta-analysis.

	Mean (h)	Median (h)	<i>SD</i>
Sample duration (overall)	6.17	1.00	9.97
Clogging: not mentioned	7.70	2.00	10.73
Clogging: mentioned	2.58	0.17	6.81
Velocity measurement: continuous	4.42	0.21	9.62
Velocity measurement: beginning or end	3.68	0.50	7.00
Velocity measurement: beginning and end	9.28	3.00	12.61

549 **Note:** Data are presented both overall and according to different factor level groups.

Draft

Figure captions

- Fig. 1.** Decreases in instantaneous filtration efficiency over time for four characteristic drift samples, with model curve fits. Clockwise from top left, sample numbers are 3, 19, 11, and 16 (see Table 1).
- Fig. 2.** The effect of suspended solids on instantaneous filtration efficiency (a) and sample durations at which the 85% filtration efficiency benchmark was met (b) for each sample set. Lines are lowess fits based on pooled data from each of the four sample sets (Table 1). Error bars represent that standard error from the mean and did not exist for Salt River samples, which all had initial filtration efficiencies < 85%.
- Fig. 3.** Deviation in suspended solid concentrations as sample filtration efficiency decreases. Values indicate the variation between net-mounted and ambient flowmeter-derived values. Average filtration efficiency is the distance of water passed by the net-mounted flowmeter relative to the ambient flowmeter over the duration of a sample.
- Fig. 4.** Sample durations of the studies included in the meta-analysis, grouped in half hour increments.

Median = 1.00 h
Mean = 6.17 h
n = 77

Number of studies

Draft

0 4 8 12 16 20 24 28 32 36 40 44 48

<https://mc06.manuscriptcentral.com/cjfas-pubs>

Sample duration (h)

Supplement 2. Transcript of key moments in the drift net clogging video, Supplement 1.

Video is from the 120-min Salt River sample on 2014-10-02 listed in Table 1 of the main text.

The scenes in this video occurred at approximately 1 h of net deployment.

0:08 s: Note that the ambient (externally-mounted) flowmeter is spinning rapidly counter-clockwise, while the net-mounted flowmeter barely spins. This is indicative of net clogging and suggests that using either flowmeter for estimating the volume of water filtered by the net will be fraught with error.

0:16 s: Drifting particles are repelled from the clogged net. Note particularly as drifting macrophyte and algal matter approaches the center of the net mouth, slows, and then is rapidly expelled over the net.

0:23 s: The net-mounted flowmeter spins slightly clockwise, indicating that water and organic matter is actually backflowing out, rather than into, the net.

Supplement 3. References included in the meta-analysis.

- Benigno, G.M., and Sommer, T.R. 2008. Just add water: sources of chironomid drift in a large river floodplain. *Hydrobiologia* **600**(1): 297–305. doi:10.1007/s10750-007-9239-2.
- Benke, A.C., Parsons, K.A., and Dhar, S.M. 1991. Population and community patterns of invertebrate drift in an unregulated Coastal Plain river. *Can. J. Fish. Aquat. Sci.* **48**(5): 811–823. doi:10.1139/F91-097.
- Bernard, D.P., Neill, W.E., and Rowe, L. 1990. Impact of mild experimental acidification on short term invertebrate drift in a sensitive British Columbia stream. *Hydrobiologia* **203**(1): 63–72. doi:10.1007/Bf00005614.
- Blanchet, S., Loot, G., Bernatchez, L., and Dodson, J.J. 2008. The effects of abiotic factors and intraspecific versus interspecific competition on the diel activity patterns of Atlantic salmon (*Salmo salar*) fry. *Can. J. Fish. Aquat. Sci.* **65**(8): 1545–1553. doi:10.1139/F08-079.
- Brewin, P.A., and Ormerod, S.J. 1994. Macroinvertebrate drift in streams of the Nepalese Himalaya. *Freshwater Biol.* **32**(3): 573–583. doi:10.1111/j.1365-2427.1994.tb01148.x.
- Bridcut, E.E. 2000. A study of terrestrial and aerial macroinvertebrates on river banks and their contribution to drifting fauna and salmonid diets in a Scottish catchment. *Hydrobiologia* **427**(1): 83–100. doi:10.1023/A:1003927331472.
- Callisto, M., and Goulart, M. 2005. Invertebrate drift along a longitudinal gradient in a neotropical stream in Serra do Cipó National Park, Brazil. *Hydrobiologia* **539**(1): 47–56. doi:10.1007/s10750-004-3245-4.

- Carman, S.M., Janssen, J., Jude, D.J., and Berg, M.B. 2006. Diel interactions between prey behaviour and feeding in an invasive fish, the round goby, in a North American river. *Freshwater Biol.* **51**(4): 742–755. doi:10.1111/j.1365-2427.2006.01527.x.
- Collier, K.J., and Quinn, J.M. 2003. Land-use influences macroinvertebrate community response following a pulse disturbance. *Freshwater Biol.* **48**(8): 1462–1481. doi:10.1046/j.1365-2427.2003.01091.x.
- Culp, J.M., Scrimgeour, G.J., and Beers, C.E. 1994. The effect of sample duration on the quantification of stream drift. *Freshwater Biol.* **31**(2): 165–173. doi:10.1111/j.1365-2427.1994.tb00850.x.
- Dahl, J., and Greenberg, L.A. 1998. Effects of fish predation and habitat type on stream benthic communities. *Hydrobiologia* **361**(1): 67–76. doi:10.1023/A%3A1003137309726.
- Dahl, J., and Greenberg, L. 1999. Effects of prey dispersal on predator-prey interactions in streams. *Freshwater Biol.* **41**(4): 771–780. doi:10.1046/j.1365-2427.1999.00422.x.
- Death, R.G., Dewson, Z.S., and James, A.B.W. 2009. Is structure or function a better measure of the effects of water abstraction on ecosystem integrity? *Freshwater Biol.* **54**(10): 2037–2050. doi:10.1111/j.1365-2427.2009.02182.x.
- Dewson, Z.S., James, A.B.W., and Death, R.G. 2007. Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biol.* **52**(2): 357–369. doi:10.1111/j.1365-2427.2006.01682.x.
- DuBois, R.B., and Plaster, S.D. 1993. Effects of lampricide treatment on macroinvertebrate drift in a small, softwater stream. *Hydrobiologia* **263**(2): 119–127. doi:10.1007/Bf00006208.

- Dudgeon, D. 1990. Benthic community structure and the effect of rotenone piscicide on invertebrate drift and standing stocks in two Papua New Guinea streams. Arch. Hydrobiol. **119**(1): 35–53.
- Dudgeon, D. 2006. The impacts of human disturbance on stream benthic invertebrates and their drift in North Sulawesi, Indonesia. Freshwater Biol. **51**(9): 1710–1729. doi:10.1111/j.1365-2427.2006.01596.x.
- Earl, S.R., and Blinn, D.W. 2003. Effects of wildfire ash on water chemistry and biota in South-Western U.S.A. streams. Freshwater Biol. **48**(6): 1015–1030. doi:10.1046/j.1365-2427.2003.01066.x.
- Forrester, G.E. 1994. Diel patterns of drift by five species of mayfly at different levels of fish predation. Can. J. Fish. Aquat. Sci. **51**(11): 2549–2557. doi:10.1139/F94-254.
- Friberg, N., Andersen, T.H., Hansen, H.O., Iversen, T.M., Jacobsen, D., Krojgaard, L., and Larsen, S.E. 1994. The effect of brown trout (*Salmo trutta* L.) in stream invertebrate drift, with special reference to *Gammarus pulex* L. Hydrobiologia **294**(2): 105–110. doi:10.1007/Bf00016850.
- Fritz, K.M., and Dodds, W.K. 2002. Macroinvertebrate assemblage structure across a tallgrass prairie stream landscape. Arch. Hydrobiol. **154**(1): 79–102. doi:10.1127/archiv-hydrobiol/154/2002/79.
- Gibbins, C.N., Vericat, D., and Batalla, R.J. 2010. Relations between invertebrate drift and flow velocity in sand-bed and riffle habitats and the limits imposed by substrate stability and benthic density. J. N. Am. Benthol. Soc. **29**(3): 945–958. doi:10.1899/09-096.1.

- Hall, R.J. 1994. Responses of benthic communities to episodic acid disturbances in a lake outflow stream at the Experimental Lakes Area, Ontario. *Can. J. Fish. Aquat. Sci.* **51**(8): 1877–1892. doi:10.1139/F94-188.
- Hansen, E.A., and Closs, G.P. 2007. Temporal consistency in the long-term spatial distribution of macroinvertebrate drift along a stream reach. *Hydrobiologia* **575**(1): 361–371. doi:10.1007/s10750-006-0384-9.
- Hay, C.H., Franti, T.G., Marx, D.B., Peters, E.J., and Hesse, L.W. 2008. Macroinvertebrate drift density in relation to abiotic factors in the Missouri River. *Hydrobiologia* **598**(1): 175–189. doi:10.1007/s10750-007-9149-3.
- Huhta, A., Muotka, T., and Tikkanen, P. 2000. Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. *Freshwater Biol.* **45**(1): 33–42. doi:10.1046/j.1365-2427.2000.00615.x.
- Ilg, C., Castella, E., Lods-Crozet, B., and Marmonier, P. 2001. Invertebrate drift and physico-chemical variables in the tributaries of the Mutt, a Swiss glacial stream. *Arch. Hydrobiol.* **151**(2): 335–352. doi:10.1127/archiv-hydrobiol/151/2001/335.
- Imbert, J.B., and Perry, J.A. 2000. Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow. *Hydrobiologia* **436**(1): 191–208. doi:10.1023/A:1026582218786.
- Jackson, J.K., Sweeney, B.W., Bott, T.L., Newbold, J.D., and Kaplan, L.A. 1994. Transport of *Bacillus thuringiensis* var. *israelensis* and its effect on drift and benthic densities of nontarget macroinvertebrates in the Susquehanna River, northern Pennsylvania. *Can. J. Fish. Aquat. Sci.* **51**(2): 295–314. doi:10.1139/F94-031.

- Jacobsen, D., and Bojsen, B. 2002. Macroinvertebrate drift in Amazon streams in relation to riparian forest cover and fish fauna. *Arch. Hydrobiol.* **155**(2): 177–197.
doi:10.1127/archiv-hydrobiol/155/2002/177.
- Jacobsen, D., Cauvy-Fraunie, S., Andino, P., Espinosa, R., Cueva, D., and Dangles, O. 2014. Runoff and the longitudinal distribution of macroinvertebrates in a glacier-fed stream: implications for the effects of global warming. *Freshwater Biol.* **59**(10): 2038–2050.
doi:10.1111/fwb.12405.
- James, A.B.W., Dewson, Z.S., and Death, R.G. 2009. The influence of flow reduction on macroinvertebrate drift density and distance in three New Zealand streams. *J. N. Am. Benthol. Soc.* **28**(1): 220–232. doi:10.1899/07-146.1.
- Jenkins, A.R., and Keeley, E.R. 2010. Bioenergetic assessment of habitat quality for stream-dwelling cutthroat trout (*Oncorhynchus clarkii bouvieri*) with implications for climate change and nutrient supplementation. *Can. J. Fish. Aquat. Sci.* **67**(2): 371–385.
doi:10.1139/F09-193.
- Jenkins, R.K.B., and Ormerod, S.J. 1996. The influence of a river bird, the dipper (*Cinclus cinclus*), on the behaviour and drift of its invertebrate prey. *Freshwater Biol.* **35**(1): 45–56. doi:10.1046/j.1365-2427.1996.d01-442.x.
- Johansen, M., Thorstad, E.B., Rikardsen, A.H., Koksvik, J.I., Ugedal, O., Jensen, A.J., Saksgard, L., and Naesje, T.F. 2010. Prey availability and juvenile Atlantic salmon feeding during winter in a regulated subarctic river subject to loss of ice cover. *Hydrobiologia* **644**(1): 217–229. doi:10.1007/s10750-010-0118-x.

- Katano, I., Negishi, J.N., Minagawa, T., Doi, H., Kawaguchi, Y., and Kayaba, Y. 2009. Longitudinal macroinvertebrate organization over contrasting discontinuities: effects of a dam and a tributary. *J. N. Am. Benthol. Soc.* **28**(2): 331–351. doi:10.1899/08-010.1.
- Kelly, D.W., and Dick, J.T.A. 2005. Introduction of the non-indigenous amphipod *Gammarus pulex* alters population dynamics and diet of juvenile trout *Salmo trutta*. *Freshwater Biol.* **50**(1): 127–140. doi:10.1111/j.1365-2427.2004.01315.x.
- Kennedy, T.A., Yackulic, C.B., Cross, W.F., Grams, P.E., Yard, M.D., and Copp, A.J. 2014. The relation between invertebrate drift and two primary controls, discharge and benthic densities, in a large regulated river. *Freshwater Biol.* **59**(3): 557–572. doi:10.1111/fwb.12285.
- Koetsier, P., and Bryan, C.F. 1992. Diel, size-differential drift patterns of three macroinvertebrate species in the lower Mississippi River, Louisiana (USA). *Hydrobiologia* **228**(3): 225–230. doi:10.1007/Bf00006589.
- Koetsier, P., Minshall, G.W., and Robinson, C.T. 1996. Benthos and macroinvertebrate drift in six streams differing in alkalinity. *Hydrobiologia* **317**(1): 41–49. doi:10.1007/Bf00013724.
- Kratz, K.W., Cooper, S.D., and Melack, J.M. 1994. Effects of single and repeated experimental acid pulses on invertebrates in a high altitude Sierra Nevada stream. *Freshwater Biol.* **32**(1): 161–183. doi:10.1111/j.1365-2427.1994.tb00875.x.
- Kruzic, L.M., Scarnecchia, D.L., and Roper, B.B. 2005. Effects of electroshocking on macroinvertebrate drift in three cold water streams. *Hydrobiologia* **539**(1): 57–67. doi:10.1007/s10750-004-3246-3.

- Lancaster, J., Hildrew, A.G., and Gjerlov, C. 1996. Invertebrate drift and longitudinal transport processes in streams. *Can. J. Fish. Aquat. Sci.* **53**(3): 572–582. doi:10.1139/f95-217.
- LaPerriere, J.D. 1994. Benthic ecology of a spring-fed river of interior Alaska. *Freshwater Biol.* **32**(2): 349–357. doi:10.1111/j.1365-2427.1994.tb01131.x.
- Larsen, S., and Ormerod, S.J. 2010. Low-level effects of inert sediments on temperate stream invertebrates. *Freshwater Biol.* **55**(2): 476–486. doi:10.1111/j.1365-2427.2009.02282.x.
- Ledger, M.E., Crowe, A.L.M., Woodward, G., and Winterbourn, M.J. 2002. Is the mobility of stream insects related to their diet? *Arch. Hydrobiol.* **154**(1): 41–59. doi:10.1127/archiv-hydrobiol/154/2002/41.
- Lee, J.O., and Hershey, A.E. 2000. Effects of aquatic bryophytes and long-term fertilization on arctic stream insects. *J. N. Am. Benthol. Soc.* **19**(4): 697–708. doi:10.2307/1468127.
- Leung, E.S., Rosenfeld, J.S., and Bernhardt, J.R. 2009. Habitat effects on invertebrate drift in a small trout stream: implications for prey availability to drift-feeding fish. *Hydrobiologia* **623**(1): 113–125. doi:10.1007/s10750-008-9652-1.
- MacNeil, C., Elwood, R.W., and Nick, J.T.A. 2000. Factors influencing the importance of *Gammarus* spp. (Crustacea: Amphipoda) in riverine salmonid diets. *Arch. Hydrobiol.* **149**(1): 87–107. doi:10.1127/archiv-hydrobiol/149/2000/87.
- March, J.G., Benstead, J.P., Pringle, C.M., and Scatena, F.N. 1998. Migratory drift of larval freshwater shrimps in two tropical streams, Puerto Rico. *Freshwater Biol.* **40**(2): 261–273. doi:10.1046/j.1365-2427.1998.00352.x.
- McIntosh, A.R., Peckarsky, B.L., and Taylor, B.W. 2002. The influence of predatory fish on mayfly drift: extrapolating from experiments to nature. *Freshwater Biol.* **47**(8): 1497–1513. doi:10.1046/j.1365-2427.2002.00889.x.

- Meissner, K., Muotka, T., and Kananen, I. 2002. Drift responses of larval blackflies and their invertebrate predators to short-term flow regulation. *Arch. Hydrobiol.* **154**(4): 529–542. doi:10.1127/archiv-hydrobiol/154/2002/529.
- Mellon, C.D., Wipfli, M.S., and Li, J.L. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, USA. *Freshwater Biol.* **53**(11): 2331–2343. doi:10.1111/j.1365-2427.2008.02039.x.
- Miller, S.W., and Judson, S. 2014. Responses of macroinvertebrate drift, benthic assemblages, and trout foraging to hydropeaking. *Can. J. Fish. Aquat. Sci.* **71**(5): 675–687. doi:10.1139/cjfas-2013-0562.
- Monaghan, K.A., and Miner, A.M. 2009. Effect of anadromous salmon redd construction on macroinvertebrate communities in a recently formed stream in coastal Alaska. *J. N. Am. Benthol. Soc.* **28**(1): 153–166. doi:10.1899/08-071.1.
- Neale, M.W., Dunbar, M.J., Jones, J.I., and Ibbotson, A.T. 2008. A comparison of the relative contributions of temporal and spatial variation in the density of drifting invertebrates in a Dorset (UK) chalk stream. *Freshwater Biol.* **53**(8): 1513–1523. doi:10.1111/j.1365-2427.2008.01981.x.
- Polivka, K.M., Friedli, L.M., and Green, E.C. 2013. Stream inflow and predation risk affect littoral habitat selection by benthic fish. *Freshwater Biol.* **58**(5): 986–994. doi:10.1111/fwb.12101.
- Principe, R.E., and Corigliano, M.D. 2006. Benthic, drifting and marginal macroinvertebrate assemblages in a lowland river: temporal and spatial variations and size structure. *Hydrobiologia* **553**(1): 303–317. doi:10.1007/s10750-005-0694-3.

- Pringle, C.M., and Ramirez, A. 1998. Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. *Freshwater Biol.* **39**(2): 359–373. doi:10.1046/j.1365-2427.1998.00311.x.
- Ramirez, A., and Pringle, C.M. 1998. Invertebrate drift and benthic community dynamics in a lowland neotropical stream, Costa Rica. *Hydrobiologia* **386**(1): 19–26. doi:10.1023/A:1003409927131.
- Ramirez, A., and Pringle, C.M. 2001. Spatial and temporal patterns of invertebrate drift in streams draining a Neotropical landscape. *Freshwater Biol.* **46**(1): 47–62. doi:10.1046/j.1365-2427.2001.00636.x.
- Riehle, M.D., and Griffith, J.S. 1993. Changes in habitat use and feeding chronology of juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter in Silver Creek, Idaho. *Can. J. Fish. Aquat. Sci.* **50**(10): 2119–2128. doi:10.1139/F93-237.
- Robinson, C.T., Tockner, K., and Burgherr, P. 2002. Seasonal patterns in macroinvertebrate drift and seston transport in streams of an alpine glacial flood plain. *Freshwater Biol.* **47**(5): 985–993. doi:10.1046/j.1365-2427.2002.00835.x.
- Robinson, C.T., Aebischer, S., and Uehlinger, U. 2004a. Immediate and habitat-specific responses of macroinvertebrates to sequential, experimental floods. *J. N. Am. Benthol. Soc.* **23**(4): 853–867. doi:10.1899/0887-3593(2004)023<0853:IAHROM>2.0.CO;2.
- Robinson, C.T., Tockner, K., and Burgherr, P. 2004b. Drift benthos relationships in the seasonal colonization dynamics of alpine streams. *Arch. Hydrobiol.* **160**(4): 447–470. doi:10.1127/0003-9136/2004/0160-0447.

- Romero, N., Gresswell, R.E., and Li, J.L. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. Can. J. Fish. Aquat. Sci. **62**(8): 1797–1807. doi:10.1139/F05-099.
- Rosenfeld, J.S., and Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Can. J. Fish. Aquat. Sci. **58**(3): 585–593. doi:10.1139/cjfas-58-3-585.
- Saltveit, S.J., Haug, L., and Brittain, J.E. 2001. Invertebrate drift in a glacial river and its non-glacial tributary. Freshwater Biol. **46**(12): 1777–1789. doi:10.1046/j.1365-2427.2001.00858.x.
- Shannon, J.P., Blinn, D.W., Benenati, P.L., and Wilson, K.P. 1996. Organic drift in a regulated desert river. Can. J. Fish. Aquat. Sci. **53**(6): 1360–1369. doi:10.1139/cjfas-53-6-1360.
- Shaw, E.A., and Richardson, J.S. 2001. Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. Can. J. Fish. Aquat. Sci. **58**(11): 2213–2221. doi:10.1139/cjfas-58-11-2213.
- Smock, L.A. 1994. Movements of invertebrates between stream channels and forested floodplains. J. N. Am. Benthol. Soc. **13**(4): 524–531. doi:10.2307/1467848.
- Ubero-Pascal, N., Torralva, M., Oliva-Paterna, F.J., and Malo, J. 2000. Seasonal and diel periodicity of the drift of pupal exuviae of chironomid (Diptera) in the Mundo River (SE Spain). Arch. Hydrobiol. **147**(2): 161–170. doi:10.1127/archiv-hydrobiol/147/1999/161.
- van Riel, M.C., van der Velde, G., and de Vaate, A.B. 2006. To conquer and persist: colonization and population development of the Ponto-Caspian amphipods *Dikerogammarus villosus* and *Chelicorophium curvispinum* on bare stone substrate in the main channel of the River Rhine. Arch. Hydrobiol. **166**(1): 23–39. doi:10.1127/003-9136/2006/0166-0023.

- Waringer, J.A. 1992. The drifting of invertebrates and particulate organic matter in an Austrian mountain brook. *Freshwater Biol.* **27**(3): 367–378. doi:10.1111/j.1365-2427.1992.tb00546.x.
- Weber, N., Bouwes, N., and Jordan, C.E. 2014. Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature. *Can. J. Fish. Aquat. Sci.* **71**(8): 1158–1170. doi:10.1139/cjfas-2013-0390.
- Zhang, Y.X., Dudgeon, D., Cheng, D.S., Thoe, W., Fok, L., Wang, Z.Y., and Lee, J.H.W. 2010. Impacts of land use and water quality on macroinvertebrate communities in the Pearl River drainage basin, China. *Hydrobiologia* **652**(1): 71–88. doi:10.1007/s10750-010-0320-x.
- Zimmerman, J.K.H., and Vondracek, B. 2006. Effects of stream enclosures on drifting invertebrates and fish growth. *J. N. Am. Benthol. Soc.* **25**(2): 453–464. doi:10.1899/0887-3593(2006)25[453:Eoseod]2.0.Co;2.