

Shredder-collector facilitation in stream detrital food webs: is there enough evidence?

Stephen B. Heard and John S. Richardson

Heard, S. B. and Richardson, J. S. Shredder-collector facilitation in stream detrital food webs: is there enough evidence? – *Oikos* 72: 359–366.

It is widely assumed that, among detritivorous stream invertebrates, shredders facilitate collectors through their role in producing particles from coarser detritus. While this hypothesis is plausible, we argue that it has not been adequately tested. It has not even been clear what information would be necessary or sufficient to document such an interaction. We outline the evidence which we believe must be sought: it must be established that collectors are particle-limited, that shredder activity produces particles, that shredder activity enhances collector performance, and that the mechanism for this enhancement lies in particle production and not some other process. We review available data that bear on these propositions, and describe a straightforward experiment which could unambiguously test the shredder-collector facilitation hypothesis.

S. B. Heard, Dept of Zoology, Univ. of British Columbia, 6270 University Blvd, Vancouver, B. C., Canada V6T 1Z4. – J. S. Richardson, Westwater Research Centre, Univ. of British Columbia, 1933 West Mall, Vancouver, B. C., Canada V6T 1Z2.

Invertebrate faunas of forest streams are often dominated by detritivores which feed on organic matter derived largely from leaf litter. Two major functional groups can be distinguished among them: shredders, which consume coarse particulate organic matter (CPOM), and collectors, which consume fine particles (FPOM) filtered from the water column or gathered from sediments. Shredders process CPOM and produce particles as they feed, and it is widely believed that shredders facilitate collectors as a result of this particle production (e.g. McDiffett 1970, Cummins et al. 1973, Cummins 1974, Berrie 1976, Short and Maslin 1977, Grafius and Anderson 1979, Vannote et al. 1980, Wallace and Merritt 1980, Wallace et al. 1982, Merritt et al. 1984, Shepard and Minshall 1984, Minshall et al. 1985, Mulholland et al. 1985, Cuffney et al. 1990, Malmqvist 1993). By “facilitation” we mean that collector growth or survival is increased by the presence of shredders either in the local stream reach or in upstream portions of the watershed. Facilitation can be posited at the population level, involving particular species of

shredders and collectors, or at a systems level involving the shredder and collector functional groups in the aggregate.

These putative shredder-collector interactions are important for at least three reasons. First, on a local scale, effects of shredders on collector performance have obvious consequences for productivity throughout stream food webs. These effects are likely to have ecological and economic implications beyond the stream itself. For instance, increased collector growth should allow greater productivity of stream fish, which in turn will benefit terrestrial piscivores and commercial and sports fisheries. In addition, the emergent adults of stream collectors can be a major resource for terrestrial and aerial insectivores, and some are also important pests – for instance, black flies.

Second, on a much larger spatial scale, shredder-collector facilitation (at the level of whole functional groups) is a major element of the River Continuum Concept (Vannote et al. 1980, Minshall et al. 1985). Under the

Accepted 27 September 1994

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ISSN 0030-1299

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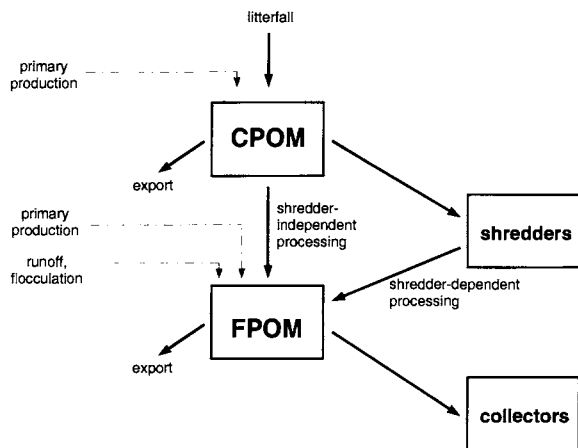


Fig. 1. A schematic representation of particulate organic matter dynamics in streams. Not shown is live "FPOM" such as drifting invertebrates, which may also be taken by collectors.

RCC, shredder activity upstream produces particles which are exported and which drive collector production in downstream reaches; such interactions highlight the necessity for a spatially integrative approach to stream and river studies. The RCC emphasizes the interdependence of stream hydrology, geology, and ecology and implies that shredder-collector interactions must be part of any effort to understand stream ecosystem function.

Third, the supposed shredder-collector facilitation is an example of a relatively understudied class of ecological interactions: processing chain interactions (Heard 1994a). In processing chain systems, resources pass through a sequence of two (or more) conditions and are exploited in each condition by a specialist consumer (or guild of consumers). The stream shredder-collector system is the most familiar of a large subset of processing chains based on particle size (Heard 1994a).

It is perhaps past time for a critical examination of the evidence supporting this potentially important interaction. Surprisingly, the widespread assumption that there are generally strong, direct, and positive links between shredders and collectors is currently not well founded. Although indirect and circumstantial evidence exists to suggest that shredder-collector facilitation is often plausible, critical experiments testing the interaction and its mechanism have been remarkably few (Winterbourn et al. 1981, Richardson and Neill 1991, Heard 1994a). Even less is known of the strength of the interaction where it exists, or of its consistency from species to species or from stream to stream.

In this paper we outline the evidence required to establish (at either the population or functional group level) that shredders facilitate collectors through their role in resource processing. Although some of this evidence is available in the literature, much of it is scanty at best. After providing some theoretical perspective, we will consider four major questions. Each of these questions

must be answered in the affirmative, for the natural system of interest, if a shredder-collector facilitation is to be established: (1) Are collectors limited by FPOM availability? (2) Does shredder feeding increase quantity and/or quality of downstream FPOM (and if so, how much)? (3) Does shredder feeding increase downstream collector growth, survivorship, or density (and if so, how much)? (4) Are we sure that the mechanism for (3) is (2)?

In a nutshell, the answers to these questions appear to be (1) sometimes, (2) probably, (3) maybe, and (4) no. However, we emphasize that the answers are likely to vary among streams and among focal shredder and collector species. While shredders may well facilitate collectors, we do not know how often or how strongly. Relatively simple experiments could shed light on this issue, but they have not been done. Below we make explicit our views on the critical questions to be addressed, the evidence available, and the directions in which to proceed.

Sources of FPOM in streams

The question of a shredder-collector interaction hinges on the availability of FPOM. Detrital FPOM (particles smaller than about 1 mm) in streams can come from several sources (Fig. 1): from runoff (Eglishaw and Shackley 1971, Hobbie and Likens 1973, Winterbourn et al. 1981, Roeding and Smock 1989), from flocculation of dissolved organic carbon (Lush and Hynes 1973, Petersen 1986), and from processing of CPOM (particles larger than 1 mm). CPOM itself, in many streams, is largely leaf litter, although in larger and non-forested streams primary producers can contribute significant amounts of organic material (e.g. Minshall 1978). Of these FPOM sources, runoff and flocculation are presumably independent of shredder activity, so the key to a putative shredder-collector interaction must lie in CPOM processing.

In the absence of shredders, FPOM is produced from CPOM by microbial action (Berrie 1976, Suberkropp and Klug 1976, Roeding and Smock 1989) and physical abrasion (Anderson and Sedell 1979, Roeding and Smock 1989). We refer to these, together, as shredder-independent processing. The rate at which such processing occurs will depend on microbial densities, and on abiotic conditions such as temperatures and flow rates (e.g. Boling et al. 1975, Iversen 1975). In particular, shredder-independent processing is presumably reduced in slow- or non-flowing water (including most laboratory microcosms) although this may be partly compensated by reduced particle export.

Shredders contribute to CPOM processing by producing faecal particles (e.g. McDiffett 1970, Shepard and Minshall 1984), and by comminuting but not ingesting CPOM (McDiffett 1970, Cummins 1973, Herbst 1982). The resulting increase in surface area may in turn allow accelerated microbial processing. We refer to all FPOM

Table 1. Estimates of FPOM removal by collectors.

| Collectors | Location | FPOM removal (%/m) | Reference |
|--|-----------------------------|--------------------|-----------------------------|
| black flies | Dorset, England | 0.0004–0.03* | Ladle et al. 1972 |
| black flies | California, USA | 0.007–0.2*§ | Maciolek and Tunzi 1968 |
| black flies | Quebec, Canada | 0.8–1.4 | Morin et al. 1988 |
| black flies + hydropsychid caddisflies | Washington/Idaho, USA | 0.01 | McCullough et al. 1979 |
| hydropsychid caddisflies | North Carolina, USA | 0.003–0.005 | Ross and Wallace 1983 |
| hydropsychid caddisflies | North Carolina, USA | 0.004–0.02 | Haefner and Wallace 1981 |
| hydropsychid caddisflies | Georgia/North Carolina, USA | 0.005 | Georgian and Wallace 1981 |
| mayflies | southern Sweden | 0.0005 | Malmqvist and Brönmark 1981 |
| unionid mussels | not reported | 0.03 | Malmqvist and Brönmark 1981 |
| lamprey larvae | southern Sweden | 0.00005 | Malmqvist and Brönmark 1981 |

* our calculation.

§ overestimate: includes removal by sedimentation.

production ultimately attributable to shredder activity as shredder-dependent processing (Fig. 1). Note that the particles produced by these various pathways may differ in quality; to correct for this, particle production rates should ideally be denoted in units such as consumer growth equivalents. We defer further discussion of particle quality until section (3) below.

The relationship between shredders, collectors, and their leaf litter resource is typical of “processing chain” systems (Heard 1994a), where changes in resource condition underlie consumer specialization. The reduction in particle size from CPOM to FPOM is the key aspect of resource condition here, and this reduction can be effected by shredder-dependent or by shredder-independent processing (Fig. 1).

Interspecific interactions in processing chains can be either amensal or commensal – that is, with one species either inhibiting or facilitating the other, but always asymmetric (Heard 1994a). The outcome in a particular case depends on the relative rates of consumer-dependent and consumer-independent processing, but also on the time scale examined: processing chain systems in general show commensal interactions on short time scales, which weaken or become amensal as more time passes (Heard 1995). A shredder-collector interaction could in theory be either amensal or commensal, because shredder-dependent processing will have complex effects on FPOM levels over time. Shredder feeding accelerates the short-term production of FPOM, but also has the opposing effect of removing CPOM that might later yield particles through shredder-independent processing. This removal includes material assimilated by shredders, and also material processed but exported from the stream reach before it can be captured by local collectors (Mulholland et al. 1985; FPOM is exported much more easily than the CPOM from which it is derived). Consequently, the fact that shredders produce particles need not mean that their activity improves net particle availability at all times. The effect of shredders on collectors, at any particular time, will depend on the net effect of shredder-dependent processing on FPOM at that time – which could be positive or negative, and will likely change with time.

The strong time-sensitivity of processing chain interactions has obvious implications for the design of shredder-collector experiments in streams. Most published experiments have been conducted over rather short time scales, relative to the generation time or main growth period of the focal insects, and the potential importance of temporal scale is generally ignored (but see Wallace et al. 1982). However, because processing chains tend to show short-term commensalisms which weaken or reverse in the longer term, neither the strength nor the sign of a facilitative interaction in a short-term experiment can be safely extrapolated to longer, natural times scales. Instead, the strength and perhaps even the sign of the shredder-collector interaction are likely to depend on the time horizon at which the interaction is evaluated – for instance, how long a shredder manipulation is run before effects on FPOM or collectors are measured. For this reason, experiments seeking to measure shredder-collector interactions, or shredder effects on resources for collectors, should ideally be run over the entire larval period of a collector cohort.

Question 1: Collector FPOM limitation

Unless collector growth or survival is actually limited by detrital FPOM, any shredder effect on its availability cannot produce an interaction. However, the degree to which stream collectors are limited by quantity or quality of FPOM remains somewhat unclear. We are unaware of any studies of resource limitation of gathering collectors in streams. There is evidence, albeit nonexperimental, that some filtering collectors may be limited by the supply of high-quality (not total or detrital) FPOM. For instance, Petersen (1987) found that net-spinning caddisfly densities in Swedish streams were related to animal seston levels, but not to total or detrital FPOM. Caddisfly growth rates can be dramatically higher on algae or zooplankton than on detrital FPOM (Richardson 1984), and high-quality animal “particles” may account for most caddisfly production, at least for larger instars (Benke

and Wallace 1980, Georgian and Wallace 1981, Brown et al. 1989). Other, less selective collectors are more likely to be limited by detrital FPOM.

It has been argued that many filter feeders are limited by space instead of by particles (e.g. Cudney and Wallace 1980, Merritt et al. 1984), although these alternatives may be difficult to distinguish (Hart 1987). The space hypothesis seems reasonable in light of the fact that filtering collectors, even in dense populations, often remove little FPOM relative to the total suspended amount (Table 1). However, because much of the FPOM in the water column will be unavailable to animals living on the bottom, low removal fractions need not rule out FPOM limitation of individual collectors. Indeed, collector density is often correlated with FPOM concentration, either among leaf packs (Short et al. 1980) or along stream reaches as FPOM quantity and quality drop away from lake outlets (Wallace and Merritt 1980, Richardson and Mackay 1991). There is also evidence for resource competition among filter feeders in local aggregations (Hart 1986, Englund 1991; but see Reice 1981), which implies that particles must be limiting at least some of the time. Richardson and Neill (1991) found coincident FPOM and collector increases after CPOM addition in artificial streams, implying FPOM limitation. In contrast, Hiltner and Hershey (1992) found decreased black fly production in an Alaska river after a fertilization treatment which increased microbial "FPOM" (among other effects); they attributed this result to competitive displacement by a caddisfly. Oddly, there appear to have been no attempts to determine responses of natural collector populations to direct FPOM supplementation. Until such experiments have been done, the FPOM-limitation picture is likely to remain confused.

Alternatively, non-competitive factors such as predation, parasitism, or abiotic conditions might limit collector populations. There have been few attempts to assess these possibilities (but see Richardson and Mackay 1991).

Question 2: Effects of shredders on CPOM and FPOM

An acceleration of CPOM processing by shredders (over shredder-independent processing rates) is a necessary, although not a sufficient, condition for a shredder-collector facilitation. Dozens of studies have compared loss rates of CPOM from microcosms or stream reaches with and without shredders. In most such studies, shredder-dependent removal of CPOM is significant (e.g. McDifft 1970, Cummins et al. 1973, Iversen 1973, Petersen and Cummins 1974, Winterbourn and Davis 1976, Davis and Winterbourn 1977, Herbst 1982, Kirby et al. 1983, Obendorfer et al. 1984, Mulholland et al. 1985, Barnes et al. 1986, Cuffney et al. 1990). Other experiments have found shredder effects on CPOM loss variable from

stream to stream (Hart and Howmiller 1975, Iversen 1975) or have found no effect at all (Mathews and Kowalczewski 1969, Kaushik and Hynes 1971, Benfield et al. 1977, Reice 1977, 1978, Richardson 1992). In some cases, this only reflects low shredder densities in the streams under study, but in others shredders were present but apparently had little influence. This lack of unanimity suggests that shredder-collector interactions are not strong everywhere.

Fewer studies have looked for increased FPOM levels in the presence of shredders. Several studies have shown increased FPOM production due to shredder activity in non-flowing laboratory microcosms, over periods of two to nine weeks (Cummins et al. 1973, Grafius and Anderson 1979, O'Hop et al. 1984). Mulholland et al. (1985) showed that a shredding snail increased FPOM in artificial stream channels over 30 weeks, although with an associated decline in particle quality (see below). Webster (1983) concluded from a simulation model that shredders were responsible for about 12% of all FPOM export in a stream in North Carolina. Finally, there have been two manipulations in natural streams. Wallace et al. (1982, 1991) used insecticide to remove all insects from two neighbouring Appalachian streams, for one and three years respectively. FPOM export from both streams dropped dramatically throughout the treatment periods. These last studies are particularly valuable, because they suggest effects of shredder feeding on FPOM production beyond the short-term effect that is always present in processing chain models (Heard 1995). However, insecticide application must have many consequences for stream communities beyond shredder removal, making the causal link somewhat uncertain, and in any case analogous data for many more streams are needed before we can judge whether the result is typical or exceptional. Shredders certainly appear unimportant in FPOM generation in some other streams (e.g. Winterbourn et al. 1981, Roeding and Smock 1989). One might expect local shredder populations to have less influence on FPOM in some streams: for instance, those where FPOM input from upstream reaches is plentiful, or those where frequent floods prevent CPOM accumulation.

An important caveat to these results is the fact that particle counts may not tell the whole story. Shredders are likely to influence particle quality as well as particle numbers. There have been no direct nutritional comparisons of the products of shredder-dependent CPOM processing and those of shredder-independent processing, probably because of the difficulty of separating the two in flowing water. There is some evidence, however, that particles produced by shredders (either in faeces or by fragmentation) may be inferior to those produced otherwise. Mulholland et al. (1985) found that bacterial abundance on FPOM (one measure of particle quality) declined with increasing shredder densities, although they could not separate particles by source. Shredder faeces may be nutritionally superior to total natural FPOM (Ward and Cummins 1979, Shepard and Minshall 1981,

Table 2. A simple experiment to test shredder-collector interactions.

| Treatment | Shredder biomass | FPOM concentration |
|--------------|------------------|--------------------|
| T1 (control) | natural | natural |
| T2 | supplemented | natural |
| T3 | natural | supplemented |
| T4 | supplemented | supplemented |

1984, but see Mattingly 1987), but worse or no better than ground leaf material (McDiffett 1970, Ward and Cummins 1979). Natural FPOM includes particle types of differing qualities, its makeup tends to be variable among stream reaches (Naiman 1983), and there is variation among shredder species and among leaf species in particle quality comparisons (Shepard and Minshall 1981). Furthermore, the most relevant comparisons are more complicated than any of these, because some shredders release uningested particles as well as faeces (McDiffett 1970, Cummins 1973, Herbst 1982), and because neither total natural FPOM nor ground leaf litter are equivalent to the products of shredder-independent processing. Experiments comparing the quality of shredder-produced FPOM to particles produced from identical CPOM in the absence of shredders are clearly called for.

Shredder manipulations and other experiments must take particle quality into account. To this end, FPOM levels should probably not be measured by simple particle counts, but rather expressed in the currency relevant to the collector species of interest – perhaps nitrogen content or collector growth performance.

Question 3: Shredder effects on collectors

Shredder improvement of FPOM availability need not guarantee facilitation of collectors. It is not clear that collectors are always particle-limited (see question (1)), and even when they are, the effect of shredders could be difficult to measure over a background of variation from other influences on particle availability and collector performance. Attempts to measure collector responses to shredder activity have been remarkably rare, despite the fact that positive responses are so widely assumed.

In non-flowing laboratory microcosms, Cummins et al. (1973) found increased growth of a mayfly in the presence of a variety of shredders, coincident with an increase in FPOM over 40–60 d. In an artificial stream experiment, Short and Maslin (1977) found that the presence of a stonefly shredder increased radiophosphorus uptake by a caddisfly and a black fly, although the experiment was terminated after 7 d, to deliberately minimize shredder-independent processing (Short and Maslin 1977: 936). It is not obvious whether these results would be realized in natural systems. Processing chain models point to the

danger in extrapolating short-term results to the longer time scales over which the growth of stream insects occurs (Heard 1995). Furthermore, experiments conducted in non-flowing microcosms may have artificially low shredder-independent processing rates and therefore overestimate the benefits to collectors of shredder activity.

We are aware of no analogous experiments manipulating shredders in natural streams. There are some observational data which may be relevant: Grafius and Anderson (1979) observed that peak black fly growth in an Oregon stream coincided seasonally with peak shredding activity, and some within-reach spatial associations of shredders and collectors have been reported (Reice 1981). These results are consistent with a shredder-collector facilitation, although there are many alternative explanations for such associations in time and space.

Question 4: Mechanisms for a shredder-collector facilitation

If a shredder-collector facilitation exists, CPOM processing is only one of many plausible mechanisms for it, and merely documenting a collector growth response to the presence of shredders would not establish any particular mechanism. Even co-occurrence of collector and FPOM increases (e.g. Cummins et al. 1973, Grafius and Anderson 1979, Richardson and Neill 1991) is only weak evidence for a processing mechanism. Other mechanisms for a shredder-collector interaction are conceivable: for instance, shredders in high densities might satiate predators that also take collectors, release sedimented particles by bioturbation, or clear leaf litter from substrate and provide attachment sites for collectors. Experiments to distinguish among possible mechanisms have not been done.

An experiment

Testing the shredder-collector facilitation hypothesis need not be a formidable proposition. A simple (at least in design) 2×2 factorial manipulation of shredders and FPOM in natural streams could, in fact, provide answers to all four of our questions. This experiment would have four treatments, each with either natural or supplemented levels of shredder biomass and FPOM (Table 2). Ideally the added FPOM should be shredder-generated, but the use of different particle sources could also provide some insight into the importance of FPOM quality. The FPOM addition should be sufficient that collectors in those treatments (T3 and T4) are not food-limited, and the duration of the experiment should ideally be matched to the larval period of the focal collector species.

The answer to question 1 is provided by contrasting

collector growth or survival (or possibly immigration less emigration) in T3 vs T1; if $T3 > T1$ then collectors are FPOM-limited. If FPOM removal rates by collectors are negligible, as Table 1 suggests, shredder effects on particle availability (question 2) can be assessed by comparing FPOM abundance (or quality) in T2 vs T1 and T4 vs T3. If FPOM removal rates are not negligible, it might be necessary to use two additional treatments differing in shredder biomass and with collectors removed or at least controlled. Shredder effects on collectors (question 3) can be measured by contrasting collector growth or survival in T2 vs T1. Finally, if the FPOM addition is sufficient that particles in those treatments are no longer limiting (collector performance is saturated), then a processing mechanism for the shredder-collector interaction (question 4) should produce a significant shredder/FPOM interaction term. A processing-mediated interaction would produce increased collector growth in the two treatments with *either* added shredders *or* added FPOM, but no further increase in the treatment with both – that is, $T2 > T1$ and $T3 > T1$, but $T4 = \max(T3, T2)$. Heard (1994b) used a similar protocol to document a processing chain commensalism between pitcher-plant midges and mosquitoes – an interaction which closely resembles the putative shredder-collector facilitation in mechanism. Other experiments which explicitly test particular aspects of our four questions would also be valuable contributions to supporting (or rejecting) the facilitation hypothesis.

Conclusions

It is clear that none of the questions we started with can be answered with any assurance. There have been too few relevant experiments, and those that have been done have too often been incomplete or of very short duration. We summarize briefly what we know, and what we do not know, about our four questions:

(1) Are collectors limited by FPOM? Probably, at least in some streams and at some times, but we do not know how often or how strongly, or whether quantity or quality is more limiting. The answers are likely to vary among collector species, and more selective collectors are likely to be limited by particular components of FPOM, which may or may not be products of shredder activity.

(2) Does shredder feeding increase downstream FPOM? Probably, in some streams and over some time scales. However, few appropriate experiments have been done, and both the presence and strength of the shredder effect are likely to be variable in space and time. The nature of shredder effects on particle quality is still unclear.

(3) Does shredder feeding increase downstream growth of collectors? In microcosms, and in artificial streams over very short time scales, at least sometimes it does. In natural populations and over appropriately long time scales, data appear to be completely lacking.

(4) Do effects on collectors, when such effects exist, result from CPOM processing? On this point, data are completely lacking.

Shredders may indeed facilitate collectors, as the conventional wisdom would have it. However, we are not close to being able to demonstrate that this assertion is true, or if appropriate, that it is false. The matter is important, not least because the putative interaction is central to some current stream ecosystem theory (e.g. Vannote et al. 1980, Minshall et al. 1985), and because of its significance for stream food web function. The critical experiments are not difficult to design and should be practical to carry out. We hope that by drawing attention to the Emperor's lack of clothes we may stimulate stream ecologists to dress him.

Acknowledgements – SBH thanks D. Fonseca for early discussion on the issue of shredders and collectors. T. Day, D. Hart, B. Malmqvist, B. Neill, J. Rosenfeld, and B. Wallace made valuable comments on the manuscript. The contribution of SBH was supported by an E. B. Eastburn postdoctoral fellowship from the Hamilton Foundation; that of JSR was supported by an operating grant from NSERC (Canada).

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