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Toward Quantifying the Relative Importance of Invertebrate Consumption and Bioturbation in Puerto Rican Streams

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ABSTRACT

Although many tropical stream consumers have large effects on resource quantity and quality, little is known about the relative importance of consumption versus bioturbation. We quantified egestion rates of freshwater shrimps (*Atya* spp. and *Xiphocaris elongata*) and mayflies (Leptophlebiidae) in two forest streams within the Luquillo Experimental Forest, Puerto Rico. Consumer body size was a strong predictor of egestion rates, with mass-specific egestion rates declining with body size and per-individual egestion rates increasing with body size. We used these egestion rates, together with published rates of epilithon removal by consumers and epilithon accrual by particle deposition and periphytic growth (*i.e.*, with and without consumer access), to estimate the importance of consumption and bioturbation after storm events and during base-flow conditions. Our estimates suggest that direct consumption of epilithon can only account for a minor proportion ($< 5\%$) of material removed following storm events, with most removal likely resulting from bioturbation. During base-flow conditions, we found that consumers (largely shrimps) may be capable of consuming a significant proportion of the material that would otherwise accrue on benthic substrata, but this result was limited to one high-elevation site. Our study suggests that bioturbation is the dominant process that redistributes and entrains fine particles after storm events, and that a variable fraction of deposited and accrued benthic material may be consumed during base-flow conditions. Our results underscore the importance of tropical stream animals in altering the benthic environment through both consumption and bioturbation, and suggest that consumer-mediated material cycling is likely to be context dependent.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: Atyidae; bioenergetics; Caribbean; Decapoda; detritus; ecosystem engineer; freshwater shrimps; island; mayflies; tropical stream.

ANIMALS PLAY IMPORTANT ROLES IN MODULATING RESOURCE AVAILABILITY AND ecosystem-level processes (Kitchell *et al.* 1979, Jones & Lawton 1994, Vanni 2002, Moore 2006). They do so either directly through consumptive and assimilatory processes, or indirectly through their effects on the physical environment (Vanni 2002). In many cases, the dominant mechanism by which animals alter resource availability is unclear. For example, *Prochilodus mariae*, a tropical detritivorous fish dramatically alters ecosystem metabolism and organic carbon flux through both consumption and bioturbation (Flecker 1996, Taylor *et al.* 2006). Yet, the relative importance of these direct and indirect activities is unknown. Similarly, freshwater shrimps and mayflies have been shown to strongly alter the quantity and quality of epilithon (*i.e.*, loosely deposited and attached inorganic and organic material) in tropical streams (Pringle *et al.* 1999, March *et al.* 2002, Moutlon *et al.* 2004, Souza & Moulton 2005), but the relative contributions of consumption and bioturbation remain ambiguous.

Many tropical rain forest streams exhibit flashy and variable hydrology in response to precipitation events (*e.g.*, Smith *et al.* 2005). These events entrain and deliver to streams large amounts of inorganic and organic material (McDowell & Ashbury 1994), reducing water clarity and disturbing the benthic environment. Directly following these events, as stream discharge returns to base flow, suspended particles are deposited onto benthic substrata. Remarkably, in many tropical streams where consumers are abundant, this deposited material is redistributed and cleared from the stream bottom within hours to days (Pringle & Blake 1994, Pringle *et al.* 1999, March *et al.* 2002). In addition, during interstorm periods the quantity of epilithic material remains consistently low until the next storm event (Pringle *et al.* 1999), despite continuous delivery of fine particles from upstream and low-levels of benthic algal production and accrual during base-flow conditions. Based on these observations and experiments, it is clear that tropical consumers strongly modulate epilithon dynamics following storms and at base flow. However, to our knowledge, no studies have attempted to quantify the relative importance of consumption versus bioturbation in tropical systems.

One approach to elucidating the relative importance of consumption and bioturbation is to isolate consumption by quantifying ingestion or egestion rates for dominant taxa. In combination with population biomass estimates, this information can be used to calculate the amount of material potentially consumed by a population per unit time. Next, these consumption rates can be compared to previously published estimates of: (1) consumer-mediated material removal rates following storm events (*i.e.*, changes in epilithon standing stocks over time; Pringle & Blake 1994, March *et al.* 2002);

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and (2) total material accrual rates in the absence of consumers during base-flow conditions (March *et al.* 2002). These comparisons facilitate a preliminary estimate of the importance of consumption versus bioturbation during two distinct phases: (1) after common storm events; and (2) during base-flow conditions. Here, we use this field-based approach to examine the potential importance of consumption versus bioturbation in redistributing and processing epilithon in tropical streams of Puerto Rico.

METHODS

QUANTIFYING INDIVIDUAL EGESTION AND CONSUMPTION RATES.—We quantified egestion rates of freshwater shrimps (*Atya* spp. and *Xiphocaris elongata* (Guérin-Méneville) and mayflies (Leptophlebiidae: *Borinquena carmencita* Traver and *Neohagenulus julio* Traver) in two forest streams within the Luquillo Experimental Forest (LEF; 18 °18′N, 65 °47′W), Puerto Rico, U.S.A.: Quebrada Prieta and Quebrada Bisley-3 (hereafter Prieta and Bisley; see Covich & McDowell 1996, Pringle *et al.* 1999, and Covich *et al.* 2003). These taxa represent the dominant primary consumers (by abundance and biomass) in many Puerto Rican streams, and the shrimps in particular are known to have strong effects on the quantity of fine particulate material (*e.g.*, Pringle & Blake 1994, Pringle *et al.* 1999, Greathouse & Pringle 2006). We chose Prieta and Bisley as study sites because these streams represent a range of fish predation (no predatory fish in Prieta, predatory fish present in Bisley), shrimp density (high in Prieta, low in Bisley), and organic and inorganic matter standing stock (low in Prieta, high in Bisley; Pringle *et al.* 1999, Crowl *et al.* 2002). Thus, our estimates of individual egestion rates span a range of conditions, facilitating the application of these rates to other streams in the LEF (see below).

Prieta and Bisley are high-gradient headwater streams that are subject to extreme changes in discharge in response to intense rainfall events throughout the year (Covich & McDowell 1996). Benthic substrata consist predominantly of large boulders and cobble, leading to a series of pools interspersed with boulder-lined riffles; fine sediments and silt are present in depositional areas of pools and between large boulders (also see Pringle *et al.* 1999 and Covich *et al.* 2003). Both streams are heavily shaded by riparian vegetation, and light limitation of algal production is likely (Mulholland *et al.* 2001, Ortiz-Zayas *et al.* 2005).

Together, *Atya* spp. (consisting of *Atya lanipes* Holthuis, *Atya scabra* (Leach), and *Atya innocuous* (Herbst)), *X. elongata* and leptophlebiid mayflies represent > 80 percent of the invertebrate biomass of many forest streams in Puerto Rico (*e.g.*, Greathouse & Pringle 2006), and include fine particulate material (*i.e.*, fine leaf detritus, algae, amorphous detritus) as a major dietary component (Covich 1988, Pringle *et al.* 1993; W. F. Cross and A. Ramírez, pers. obs.). The shrimp assemblage in Prieta is dominated by *A. lanipes* (~60%) and *X. elongata* (~40%) at relatively high densities (~15–20/m^2; Covich *et al.* 2003; A. P. Covich, T. A. Crowl, and W. F. Cross, pers. obs.); densities in Bisley are roughly an order of magnitude lower than those in Prieta and consist of predominantly *X. elongata* (~50%) and *Macrobrachium* spp. (~50%). In this study, we did not quantify egestion rates of *Macrobrachium* spp. because their densities tend to be lower than *Atya* spp. and *X. elongata*, and they are often more carnivorous than the other taxa (*e.g.*, Covich & McDowell 1996, Mantel & Dudgeon 2004; W. F. Cross, pers. obs.). As such, their direct influence on dynamics of fine particulate material is likely to be low.

Egestion rates were quantified during daylight hours (generally between 1000 and 1600) in both streams on five dates during June and July 2005. Invertebrates of a range of sizes were collected by hand or dipnet, rinsed, and placed individually (shrimps) or in groups (mayflies, groups of 20–40 individuals) into 1L plastic bags with 200 ml filtered (using Whatman GF/C filters) stream water. Bags were incubated for 1–2 h in the stream (mean temperature 22–23°C), invertebrates were removed, and egested material was filtered onto precombusted glass fiber filters (Whatman GF/C). Invertebrates and filters were dried separately at 60°C and weighed to obtain dry mass (DM). Filters were then ashed at 500°C to obtain ash-free dry mass (AFDM; *i.e.*, organic matter). Mass-specific egestion rates were calculated as g AFDM egested/g animal DM/hour . Per-individual egestion rates were calculated as g AFDM egested/hour. This method may significantly underestimate rates of egestion if consumers eat their own feces during the incubations, or rates of egestion decline over time for temporarily starved individuals. We cannot completely rule out these possibilities. However, we found no relationship between length of incubation and egestion rate ($R < 0.1$; $N = 67$), suggesting no significant decline in egestion over the relatively short incubation periods. Nonetheless, any error introduced by these issues would result in underestimation of total consumption, making our conclusions about total egestion (and consumption) by consumer populations relatively conservative.

ESTIMATING THE IMPORTANCE OF CONSUMPTION VS. BIOTURBATION.—Previous studies in LEF streams have used a novel electric exclusion technique to experimentally exclude macroconsumers from plots without altering local hydrology or fine particle dynamics. These previous studies permit an analysis of: (1) consumer-mediated epilithon removal rates following storm events (Pringle & Blake 1994, March *et al.* 2002); and (2) epilithon accrual rates at base flow in the absence of consumers (March *et al.* 2002). Removal rates following storm events represent the total removal of material by consumers, which includes both consumption and bioturbation. Thus the difference between our estimates of total consumption rate (see below) and the total removal rate should approximate material loss due to bioturbation after storm events. Accrual rates during base flow (in the absence of consumers; March *et al.* 2002) represent the accumulation of epilithon (both deposited material and accrued algal and microbial biomass) with no consumption or bioturbation. Again, by comparing our estimates of total consumption rate with the total accrual rate, we can approximate the importance of bioturbation in the removal of fine benthic material during base-flow conditions.

To estimate epilithon removal rates from previous studies, we calculated the change per hour in epilithon standing stock following: (1) a storm event, in which a large amount of fine particulate

TABLE 1. *Estimates of the contribution of consumption to epilithon removal after storm events and during base flow. Egestion rates are from this study. Consumer biomass, removal rates, and accrual rates are from March* et al. *(2002) and Pringle and Blake (1994). 'Atya' refers to all species of Atya, but is predominantly* Atya lanipes. *'Xipho' refers to* Xiphocaris elongata. *DM = dry mass; AFDM = ash-free dry mass; CI = confidence interval.*

	Quebrada Sonadora	Espiritu Santo	Quebrada Toronja
Number observed per tile or hoop (Atya, Xipho)	0.25, 0.25[a]	0, 0.3[a]	2.7, 2.0[b]
Tile or hoop size (m^2)	0.0105[a]	0.0105[a]	0.08[b]
Shrimp density (no./m^2; Atya, Xipho)	23.8, 23.8[a]	0, 28.6[a]	34.0, 25.0[b]
Mean biomass of individuals (g DM; Atya, Xipho)	0.32, 0.24[a]	0.32, 0.24[a]	0.52, 0.32[b]
Shrimp biomass (g DM/m^2; Atya, Xipho)	7.6, 5.7	0, 6.9	17.7, 8.0[b]
Total shrimp biomass (g DM/m^2)	13.33[a]	6.91[a]	25.38[b]
Mayfly biomass (g DM/m^2)	0.022[a]	0.008[a]	—
Egestion rate ± 95% CI (shrimps, g DM/g DM/h)	0.005 ± 0.001	0.005 ± 0.001	0.005 ± 0.001
Egestion rate ± 95% CI (shrimps, g AFDM/g DM/h)	0.0037 ± 0.0007	0.0037 ± 0.0007	0.0037 ± 0.0007
Egestion rate ± 95% CI (mayflies, g DM/g DM/h)	0.3518 ± 0.1727	0.3518 ± 0.1727	0.3518 ± 0.1727
Egestion rate ± 95% CI rate (mayflies, g AFDM/g DM/h)	0.3310 ± 0.1943	0.3310 ± 0.1943	0.3310 ± 0.1943
Total egestion ± 95% CI (g DM/m^2/h)	0.0744 ± 0.0171	0.0374 ± 0.0083	0.1269 ± 0.0254
Total egestion ± 95% CI (g AFDM/m^2/h)	0.0566 ± 0.0136	0.0282 ± 0.0064	0.0939 ± 0.0178
DM (g/m^2) without shrimps (electricity on)	63[a]	129[a]	140[b]
DM (g/m^2) with shrimps (electricity off)	11[a]	41[a]	19[b]
AFDM (g/m^2) without shrimps (electricity on)	14[a]	21[a]	28[b]
AFDM (g/m^2) with shrimps (electricity off)	2.5[a]	7[a]	4[b]
Elapsed time (h) after shrimp access	24	24	24
Epilithon removal rate (g DM/m^2/h)	2.2[a]	3.7[a]	5.1[b]
Epilithon removal rate (g AFDM/m^2/h)	0.48[a]	0.59[a]	1.02[b]
After storm events			
% epilithon removal attributable to consumption (DM)	3.4 ± 0.8	1.0 ± 0.2	2.5 ± 0.5
% epilithon removal attributable to consumption (AFDM)	11.8 ± 2.8	4.7 ± 0.9	9.2 ± 1.8
Epilithon accrual rate (g DM/m^2/h)	0.10[a]	0.50[a]	
Epilithon accrual rate (g AFDM/m^2/h)	0.02[a]	0.10[a]	
At base flow			
Potential % of accrual consumed (DM)	74.4 ± 17.1	7.5 ± 1.6	
Potential % of accrual consumed (AFDM)	283 ± 68.0	28.2 ± 6.4	

[a] From March *et al.* 2002; Total shrimp abundance is from observations in table 3. Abundance was split evenly between *Atya* and *Xiphocaris* in Quebrada Sonadora and allocated to *Xiphocaris* in Espiritu Santo. Average shrimp sizes reported in table 1 were used to calculate individual biomass with carapace length–weight regressions (W. F. Cross, pers. obs.). We calculated epilithon removal rate as the average change in epilithon standing stock (DM and AFDM) per hour after consumers were allowed access to electric exclusion plots (see figs. 1 and 2 in March *et al.* 2002). Epilithon accrual rate was calculated from average changes in epilithon DM and AFDM over time in the shrimp-excluded plots (fig. 1, March *et al.* 2002). Raw data were provided by J. G. March, Washington and Jefferson College, Pennsylvania.

[b] From Pringle and Blake (1994); Shrimp abundance is from observations in table 1. Individuals were assumed to be average size based on personal communication, A. P. Covich, University of Georgia. We calculated epilithon removal rate as the average change in epilithon standing stock (DM and AFDM) in control plots following a single storm event (between hours 6 and 30 in Fig. 3). Based on March *et al.* (2002), and additional personal observation (W. F. Cross), we assumed AFDM was, on average, 20 percent of DM. Data from Pringle and Blake were extracted using GraphClick (Arizona Software, http://www.arizona-software.ch/). Note that calculations using the above numbers may produce slightly different results than reported here because of rounding errors.

material was deposited (Pringle & Blake 1994; 6–30 h following the storm); and (2) invertebrate access to an area in which invertebrates were previously excluded with electricity (March *et al.* 2002; days 37 and 38). In the March *et al.* (2002) study, we assumed that epilithon standing stocks measured on day 35 was equivalent to day 37, when invertebrates were allowed access to excluded plots. To estimate epilithon accrual rates in the absence of invertebrates (and during base flow), we calculated the change per hour in epilithon standing stock following experimental invertebrate exclusion (March *et al.* 2002; between days 15 and 30). Additional data used in our calculations are presented in Table 1.

For each taxonomic group, total consumption of epilithic material (DM or AFDM) per unit time was calculated as the product of mean mass-specific egestion rate (from our study) and consumer biomass (g DM/m^2, as determined in March *et al.* 2002 and Pringle & Blake 1994; Table 1). To estimate a realistic range of total consumption, and to account for potential errors in our egestion rate estimates, we used egestion rates that corresponded to the upper and lower 95% CIs. We made three important assumptions when estimating total consumption. First, we assumed that egestion rate and consumption rate were identical (see Cammen 1980). Following Cammen (1980), assuming 20 percent organic matter content of bulk epilithon (an average based on March *et al.* 2002) and 10 percent assimilation efficiency of silt/detritus, egestion rates likely underestimated consumption by only 2 percent. Error introduced by this assumption is far outweighed by error in shrimp biomass estimates. Second, we assumed that consumer diets consisted of 100 percent epilithon (inclusive of detritus, algae, inorganic sediment, and colloidal organic matter). In Puerto Rican headwater streams, this assumption is reasonable for *Atya* spp. (Covich 1988, March & Pringle 2003) and leptophlebiid mayflies (A. Ramírez, pers. obs.), but *X. elongata* is also known to consume larger particles of leaf litter and, to a lesser extent, animal prey (Covich & McDowell 1996, Crowl *et al.* 2001, March *et al.* 2001, March & Pringle 2003). As such, our calculations should be viewed as conservative estimates of potential epilithon consumption. Our third assumption was that consumers eat bulk epilithon nonselectively, which we cannot sufficiently evaluate at this point, but the presence of some degree of selectivity is likely to be the case (*e.g.*, Merriam *et al.* 2002, March & Pringle 2003, Brito *et al.* 2006).

We compared our estimates of total consumption per hour to the aforementioned estimates of epilithon removal and accrual rates in three streams within the LEF: Quebrada Toronja, Quebrada Sonadora, and Rio Espiritu Santo (Pringle & Blake 1994, March *et al.* 2002). Quebrada Toronja, a first-order tributary of Quebrada Sonadora is heavily shaded, and resembles Prieta and Bisley in size and community structure. Quebrada Sonadora and Espiritu Santo are considerably larger streams (~third to fourth order) with open canopies, high incident light, and possibly higher primary production (Ortiz-Zayas *et al.* 2005). Benthic substrata and habitat types are relatively similar among these streams.

Our estimates of the relative importance of consumption and bioturbation are limited to a few case studies in selected LEF streams. Thus, for heuristic purposes, we explored a general relationship between shrimp biomass and total consumption using a wide range in individual consumption rates that correspond to the 95% CIs of our egestion rate data. This analysis allowed us to examine the likely contributions of consumption and bioturbation during base flow and after storm events across a broad range of potential shrimp biomass (0–20 g DM/m^2).

Statistical analysis.—Comparisons of egestion rates between species and streams were done with two-way ANCOVA using body size (DM) as the covariate. Regression analysis was used to examine the relationship between shrimp body size and egestion rates. Two-tailed *t*-tests were used to test for differences between streams in mayfly egestion rates. Where necessary, data were log(x + 1) transformed to meet assumptions of normality and homogeneity of variance.

RESULTS

Mass-specific egestion rates of freshwater shrimps averaged 0.0037 g AFDM/g DM/h and ranged from 0.0005 to 0.0126 g AFDM/g DM/h (Fig. 1A). A large component of the variation in mass-specific egestion rate was explained by shrimp body size ($R^2 = 0.49$; $P < 0.0001$), with mass-specific egestion rates declining with increasing shrimp body size (Fig. 1A). On a per-individual basis, egestion rates increased with body size ($R^2 = 0.30$; $P < 0.0001$; Fig. 1B).

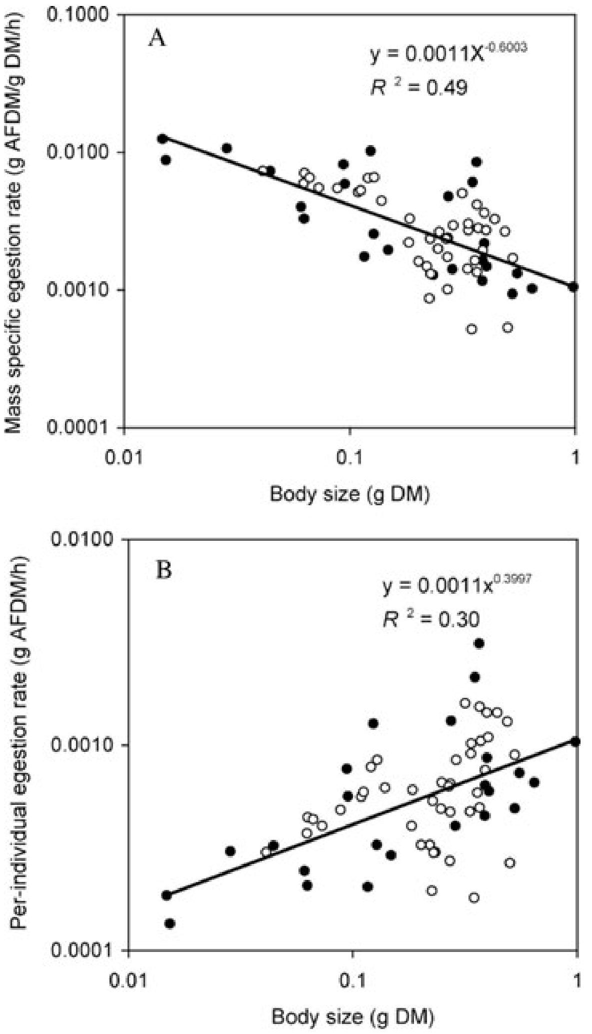

FIGURE 1. (A) Mass-specific egestion rates (g AFDM/g DM/h) and (B) per-individual egestion rates (g AFDM/h) of *Atya* spp. (black circles) and *Xiphocaris elongata* (white circles) across a range of body size (g DM). The power equations describe the combined relationship for both taxa. Egestion rates did not differ significantly between streams (see text). One statistical outlier was removed from these relationships.

Variability in egestion rates among individuals was relatively high, particularly for larger individuals (Fig. 1). Overall, there was no difference in mass-specific or per-individual egestion rates between streams (ANCOVA; $P > 0.05$), but *Atya* spp. had significantly higher mass-specific egestion rates than *X. elongata* (ANCOVA; $P < 0.05$). This between-taxon difference was likely driven by high mass-specific egestion rates of a few small individuals of *Atya* spp., and no representation of very small *X. elongata* (Fig. 1A). When per-individual rates were analyzed separately by taxonomic group, relationships remained significant for both *Atya* spp. ($R^2 = 0.42$, $P < 0.05$) and *X. elongata* ($R^2 = 0.14$, $P < 0.05$), although the amount of variation in egestion rates explained by size was low for *X. elongata*. Mass-specific egestion rates expressed on a dry mass basis averaged 0.005 g AFDM/g DM/h and ranged from 0.0001 to 0.0282. The significance and patterns of size-specific egestion based rates on dry mass were nearly identical (data not shown).

Mass-specific egestion rates of leptophlebiid mayflies were nearly two orders of magnitude higher than shrimps (mean: 0.3310 g AFDM/g DM/h; range: 0.02–1.13 g AFDM/g DM/h). There was no significant difference in mayfly egestion rates between streams (*t*-test; $P > 0.05$). Because mayfly egestion rates were quantified from groups of individuals, per-individual rates and size-specific rates were not calculated.

To examine the relative importance of consumption and bioturbation in removal of epilithon in three LEF streams with variable shrimp biomass, we combined our estimates of mass-specific egestion rates with previously published data on consumer biomass and epilithon removal and accrual rates from three nearby streams in the LEF (Pringle & Blake 1994, March *et al.* 2002; Table 1). Based on March *et al.* (2002) and Pringle and Blake (1994), epilithon was removed by consumers after storm events at a rate of 2.2–5.1 g DM/m^2/h. Our estimates suggest that direct consumption during this time could only account for < 5 percent of the dry mass removed, and < 12 percent of the organic matter removed from rock substrates (Table 1). The remainder was likely removed by nonconsumptive bioturbation activities of shrimps, which attain high biomass in the three streams analyzed (Table 1). In contrast, our calculations revealed that, during base-flow conditions, shrimps and mayflies are capable of consuming an average of 74 percent of the epilithon that would otherwise accrue at the high altitude site (Quebrada Sonadora), and 7.5 percent of this material further downstream (Espiritu Santo; Table 1). Consumption of organic matter during base-flow conditions was considerably higher, and in Quebrada Sonadora, exceeded our estimates of organic matter accrual (Table 1).

Using a realistic range of organic matter consumption rates (95% CI based on our data: 0.0030–0.0044 g AFDM/g DM/h), we calculated total potential consumption by shrimps (the dominant consumer) across a broad range of shrimp biomass (Fig. 2). We then compared this range of consumption to the literature-based ranges in organic matter accrual at base flow and organic matter removal after storm events (Pringle & Blake 1994, March *et al.* 2002). Our analysis suggests that during base-flow conditions, consumption by shrimps is within the range of organic matter accrual rates (*i.e.*, consumption may equal accrual) above a shrimp biomass of *ca* 4.5 g DM/m^2 (Fig. 2). Below this level of shrimp biomass, it is likely that accrual will exceed consumption. In contrast, after storm events, extremely high sediment removal rates (0.48–1.02 g AFDM/m^2/h; Table 1) suggest that shrimp consumption may be negligible. Results from an analysis based on dry mass instead of ash-free dry mass were qualitatively similar (data not shown).

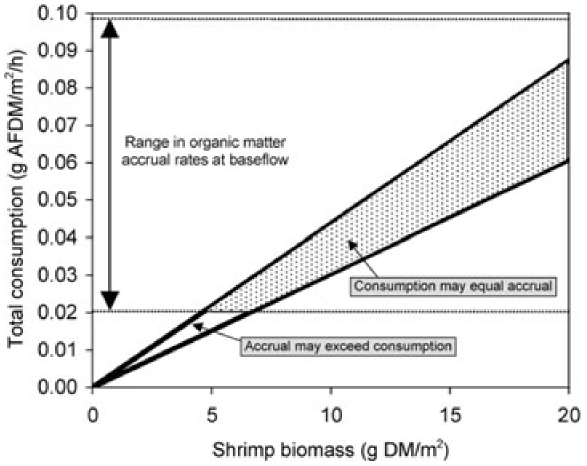

FIGURE 2. Heuristic model showing predicted shrimp consumption rates across a broad range in shrimp biomass. The dark lines represent the upper and lower boundaries in individual consumption rate based on the 95% CIs of measured egestion rates. Dotted lines represent the range in organic matter accrual rates calculated from March *et al.* (2002). The dotted area between the dark lines represents conditions where shrimp consumption rates may exceed accrual rates.

DISCUSSION

Although a number of studies have shown strong effects of tropical stream consumers on benthic organic matter and invertebrates (*e.g.*, Flecker 1996, Pringle *et al.* 1999, March *et al.* 2002, Souza & Moulton 2005, Taylor *et al.* 2006), few have attempted to quantify whether these changes were driven by direct consumption or nonconsumptive bioturbation (but see Scrimgeour *et al.* 1991, Lamberti *et al.* 1989 for examples from temperate streams). Identifying the relative importance of these processes, as well as how they vary spatially and temporally, will increase our understanding of the direct and indirect effects of consumers on material cycling in tropical stream ecosystems. Our study, which combined individual egestion rates with published rates of epilithon removal and accrual rates, suggests that the relative importance of consumption and bioturbation is context dependent. Specifically, bioturbation appears to dominate after storm events, and consumption is likely to be more important during base-flow conditions in streams where shrimp are abundant. Moreover, there appears to be a consumer biomass threshold (~4–5 g DM/m^2) below which shrimps in Puerto Rican streams are predicted to have little influence on epilithon dynamics based on consumption alone. For example, Pringle *et al.* (1999) found no net increase in epilithon accrual with the exclusion of macroconsumers in Bisley, where shrimp abundance is extremely low.

After storm events, shrimps rapidly clear deposited fine material from benthic substrata (Pringle & Blake 1994, March *et al.* 2002, Greathouse *et al.* 2006a). In Puerto Rican streams with relatively high consumer biomass, the quantity of epilithon often returns to prestorm levels within hours to days (Pringle & Blake 1994; W. F. Cross pers. obs.). Our study suggests that very little of this removed material actually passes through the guts of consumers, and that the majority is either redistributed within the stream reach or exported downstream via bioturbation. Poststorm removal rates ranged from 2.2 to 5.1 g DM/m^2/h (Table 1; Pringle & Blake 1994, March *et al.* 2002), which far exceeded our estimates of consumption rates (0.074–0.127 g DM/m^2/h). In fact, even if our estimates of consumption were off by an order of magnitude, the rapid clearing of benthic substrata could not be accounted for by direct consumption. The fate of the removed material, however, is not clear. Whether it is redistributed (*i.e.*, into rock crevices, stream margins, etc.) or exported will likely depend on the local flow environment, with downstream export predicted to be most important in fast-flowing, erosive habitats.

In Quebrada Sondadora and Espiritu Santo, we calculated the poststorm epilithon removal attributable to consumption by assuming that shrimp density during the 24 h following consumer exclusion was similar to average densities in control plots (see table 3 in March *et al.* 2002). However, in experiments where electric exclusion is employed, shrimps tend to congregate on the 'resource islands' from which they were previously excluded, at least for the first hour following experimental exclusion (see table 4 in March *et al.* 2002; J. G. March, pers. comm.). As such, our estimates of removal due to consumption may be slightly biased low at Quebrada Sonadora. For example, if we assume that densities at Quebrada Sonadora were 1.5 instead of 0.5 shrimps per tile over the 24 h following exclusion, the percent of DM removal attributed to consumption increases from 3.4 percent (Table 1) to ~9.7 percent. Nonetheless, our estimates of removal due to consumption after storm events remain relatively low.

Between storm events, where consumers are abundant, the quantity of epilithon remains consistently low (Pringle *et al.* 1999, March *et al.* 2002). During these time periods, material inputs (*i.e.*, from upstream or from algal and microbial production) must be roughly balanced with material export (*i.e.*, consumption, respiration, downstream export, and redistribution). March *et al.* (2002) excluded consumers with electricity which allowed us to calculate epilithon accrual (*i.e.*, input) rates in the absence of consumers in multiple Puerto Rican streams. These inputs include material deposited from the water column as well as production of periphytic algae and heterotrophic microbes. Our estimates of potential consumption overlap with these input rates at relatively high levels of consumer biomass (Fig. 2), suggesting that consumption may be quantitatively important during base-flow conditions. If the quality of organic material is altered by passing through the gut of a consumer (Wotton & Malmqvist 2001), base-flow conditions may represent critical times of consumer-mediated organic matter processing and nutrient mineralization and recycling.

Previous studies in temperate streams have shown that nonconsumptive loss of epilithic material (versus consumption) increases with productivity or epilithon biomass. For example, both Scrimgeour *et al.* (1991) and Lamberti *et al.* (1989) found that loss of epilithon due to factors other than consumption (*e.g.*, bioturbation) increased with biomass and productivity of epilithic algae. In Puerto Rican streams, poststorm conditions represent times of high epilithic biomass, and the dominance of bioturbation during these times is consistent with previous research in temperate streams.

Although bioturbation by consumers does not directly influence the quality of organic matter, sediment clearing and redistribution has large effects on the composition and nutrient content of bulk epilithic material. In Puerto Rico, both observational (Greathouse *et al.* 2006b) and experimental (Pringle *et al.* 1999, Greathouse *et al.* 2006a) studies have shown that shrimps increase the nutrient content of epilithon by removing loosely attached low-nutrient particulate material and inorganic sediment. The remaining benthic material is often composed of a tightly adhering nutrient-rich biofilm with a significant algal component. Because epilithon quantity and quality can strongly influence the uptake and cycling of carbon and nutrients in streams (Dodds *et al.* 2004), bioturbation by shrimps likely influences ecosystem-level material cycling (*e.g.*, Taylor *et al.* 2006). Shrimp bioturbation may also have positive effects on population dynamics of invertebrate scrapers that consume nutrient-rich biofilm (*e.g.*, March *et al.* 2002, Souza & Moulton 2005). For example, growth rates of mayflies are highest in streams where shrimps are most abundant (A. Ramírez, unpublished data).

We found that mass-specific egestion rates were much higher for small individuals (*i.e.*, mayflies and small shrimps) than large individuals (see also Shepard & Minshall 1984), and patterns followed a typical negative logarithmic distribution with body size. Small-sized organisms have relatively high metabolic requirements and can process a greater amount of material per unit weight than larger animals. Because of this pattern in metabolic rates, streams with similar invertebrate biomass, but different assemblage size structure (*i.e.*, large shrimps vs. small insects or large vs. small shrimps) may exhibit strongly contrasting rates of organic matter cycling (Hall *et al.* 2007). For example, if the shrimp assemblage at Quebrada Sonadora consisted entirely of small individuals (~0.02 g DM), total assemblage egestion holding biomass constant would be an order of magnitude higher (0.13 g DM/m^2/h) than if the assemblage consisted entirely of large (~1 g DM) individuals (0.012 g DM/m^2/h). If average body size is density dependent, as is the case for many animal populations (Brown *et al.* 2004), high densities, and the consequent small average body size, may increase the importance of animals in total material processing.

On a per individual basis (instead of per weight), large shrimps processed considerably more organic matter than smaller shrimp (Fig. 1B). Thus, if biomass is not held constant, an assemblage consisting of a given number of large individuals will process a greater amount of material than one consisting of the same number of small individuals. Although we did not take population size structure into account when calculating total egestion (Table 1), differences in shrimp size frequency distributions among the streams we examined are generally minimal (W. F. Cross and A. P. Covich, University of Georgia, T. A. Crowl, Utah State University, pers. comm.). The ecosystem-level consequences of linkages among body size, community size structure and ecological processes represent an exciting avenue for future research (Brown *et al.* 2004, Woodward *et al.* 2005).

Aquatic insects are conspicuous components of tropical stream ecosystems, even in those streams that are dominated by fish and shrimp species (Ramírez & Hernández-Cruz 2004). However, our understanding of their role as consumers within streams is limited and we know much more about the influence of fishes and shrimps on ecosystem processes. Benthic insects in tropical streams tend to be smaller in size and their abundance and productivity may be low relative to temperate streams (Ramírez & Pringle 1998). In our study, mayflies had high mass-specific consumption rates relative to shrimps, but their biomass in many LEF streams is low relative to other consumers (March *et al.* 2002, Ramírez & Hernández-Cruz 2004, Greathouse & Pringle 2006). Thus, mayflies may not play a major role in processing fine particles in LEF streams. In contrast, studies in other tropical areas where insects are dominant stream components indicate that their consumptive ability can be important in controlling benthic algal biomass. For example, in Brazil and in streams draining the Pacific slope of Costa Rica, insects exert strong consumptive control on benthic periphyton biomass (Moulton *et al.* 2004, Barbee 2005).

Our method for estimating individual egestion rates may over- or underestimate *in situ* egestion rates, and therefore requires some caveats. For example, invertebrates may defecate upon capture because of handling stress, which would lead to overestimates of egestion rate. On the other hand, if invertebrates consume their own feces during incubations or if egestion slows down during the brief period of starvation, egestion rates may be underestimated. Furthermore, our egestion rates were quantified during daylight hours which may differ from rates measured in night. Although we cannot rule out these possibilities, errors introduced by these methodological limitations would not influence our general conclusions because total consumption rates are most sensitive to total consumer biomass (as opposed to smaller differences in individual egestion rates, assimilation, etc.; Fig. 2). In addition, we did not observe defecation upon capture, and there was no relationship ($R < 0.1$; $N = 67$) between incubation time and egestion rate in our study. Nonetheless, the high amount of variability among individuals may have been driven by any one or a combination of these factors.

Overall, our study shows that tropical benthic invertebrates play an important role in the movement and dynamics of fine particles in streams. After storm events, rapid removal rates are primarily accomplished by nonconsumptive bioturbation. During interstorm periods, consumption and repackaging of fine benthic material by consumers may be significant, and has potentially large implications for altering the quality of basal resources in the system, as well as material exported downstream. Future large-scale consumer manipulations (*e.g.*, Taylor *et al.* 2006) will be critical for identifying the ecosystem-level importance of consumption and bioturbation by tropical stream invertebrates.

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