LOW DENSITIES AND EXTIRPATION OF FRESHWATER SHRIMPS ASSEMBLAGES DISRUPT ECOSYSTEM-LEVEL PROPERTIES AND PROCESSES IN HIGH ELEVATION STREAMS IN PUERTO RICO

by

PEDRO JAVIER TORRES

(Under the Direction of Catherine M. Pringle)

ABSTRACT

In the tropical headwater streams of Puerto Rico, most ecosystem processes are linked to the consumer assemblages dominated by freshwater shrimps. Shrimp assemblages are known to regulate organic matter processing, nutrient cycling, biomass and production of benthic algae, and benthic organic matter levels. This strong influence on ecosystem-level processes and properties is a result of their diverse feeding mechanisms and high abundance. The effects of shrimps on ecosystem properties and processes at the reach scale are well known through multiple studies using small-scale experimental manipulations to control their presence and abundance. However, their natural distribution and abundance can be determined by geomorphological and anthropogenic features within the watershed, and data describing their ecosystem-level role at larger spatial and temporal scales are scarce. For the first part of my dissertation, I looked at long-term and large spatial scale patterns of shrimp top-down control on benthic resources in two streams with contrasting shrimp densities. My results confirm that shrimp density is a primary factor regulating (a)benthic algae, (b) benthic organic matter, and (c)inorganic sediment in high elevation streams. Secondly, I looked at the landscape scale effects of shrimp extirpations across the island and how this affect the ecosystem processes of decomposition and nutrient cycling. I used reach-scale manipulations and landscape-scale experiments to measure these processes and contrast high-elevation streams located above large dams where shrimps have been completely extirpated and streams without a downstream dam where shrimps are found in high densities and their top-down control remains unaltered. Decomposition rate was significantly higher in all streams where shrimps were present. However, there was no significant difference in nitrogen cycling between streams because of shrimp extirpations. Phosphorus uptake was significantly higher in streams above large dams where shrimps are absent. I was able to show the large spatial and temporal extent of the importance of shrimp assemblages to the function of stream ecosystems in Puerto Rico. This work is a valuable contribution to future management and conservation efforts to restore shrimp populations and ecosystem integrity across the island.

INDEX WORDS: stream consumers; top-down control; algae; decomposition; nutrient cycling; ecosystem processes; Puerto Rico

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DEDICATION

To Piper.

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CHAPTER 1

INTRODUCTION

Consumers can regulate ecosystem-level properties and processes in aquatic ecosystems at various scales. Therefore, losing of key functional species results in substantial negative ecosystem-level effects. This has been well established in stream ecosystems where losing a dominant consumer assemblage can significantly alter ecosystem processes (Taylor et al. 2006, Vaughn 2010, Whiles et al. 2013). Tropical stream ecosystem processes are often linked and regulated by their macroconsumer communities (Pringle et al. 1993, Pringle and Blake 1994, Pringle 1996, Pringle and Hamazaki 1997, Pringle et al. 1999, Crowl et al. 2001b, Covich et al. 2004, Ranvestel et al. 2004, Connelly et al. 2008, Whiles et al. 2013) making them the ideal scenario to explore the consequences of losing a consumer species or assemblage on ecosystem level properties and processes.

The native stream macroconsumer community in Puerto Rico is composed by ten species of fish, one species of crab, and seventeen species of freshwater shrimps. All of the native macroconsumers, with the exception of the lone species of freshwater crab (E*pilobocera sinuatifrons*) are migratory. With most of these being amphidromous, including all shrimp species, they require a connection between their freshwater habitats and the ocean to complete their life cycles (Smith et al. 2003). In the shrimp amphidromous life cycle, adults live in high elevation headwater streams. Females carry the eggs until they hatch, then the larvae drifts passively downstream into the estuary where metamorphosis occurs. Post larvae then crawl back into the river mouth and upstream to the headwaters to complete the cycle (Chace and Hobbs 1969). In headwater streams, freshwater shrimps are the dominant macroconsumer assemblage. These are often found in high abundances (>20 individuals m^{-2}) and represent the majority of the animal community biomass (Pringle et al. 1993, Covich and McDowell 1996, Covich et al. 2009, Hein et al. 2011).

Due to their high dominance and diverse feeding mechanisms (scraping, grazing, filtering), these have been linked to many ecosystem processes through their strong top-down control. For example, they are known to: (1) decrease algae standing stock and fine benthic organic matter (FBOM) levels (Pringle et al. 1993, Pringle 1996, Pringle et al. 1999, Greathouse et al. 2005, Greathouse et al. 2006b), (2) decrease benthic inorganic sediment levels (Pringle et al. 1999, Cross et al. 2008b), (3) increase leaf litter breakdown rates (Crowl et al. 2001b, March et al. 2001, Wright and Covich 2005), (4) influence the composition of insect assemblages (Crowl et al. 2001a, March et al. 2002, Ramirez and Hernandez-Cruz 2004), and (5) influence the downstream transport, availability, and cycling of dissolved nutrients (Crowl et al. 2001b, Benstead et al. 2010). Most of these studies describing the ecological importance of shrimps have been manipulative experiments at small (reach) scales. Only a few have looked at how these patterns translate to large spatial and temporal scales (Greathouse et al. 2006a, Greathouse et al. 2006b).

There are two major factors affecting shrimp distribution and abundance. First, the topography of the landscape and the presence of waterfalls. While waterfalls do not affect the upstream migration of shrimps, these effectively block the upstream passage to their fish predators (e.g. American eel, mountain mullet). The presence of a waterfall thus represents a predatory-free habitat in streams above them where shrimps can reach extremely high abundances (up to 50 individuals m^{-2}) and their ecosystem-level effects are stronger (Pringle 1996, Pringle et al. 1999, March et al. 2001, March et al. 2002, Anderson et al. 2008, Cross et al. 2008a, Covich et al. 2009). Second, large dams are known to act as impermeable barriers that completely block the migration pathway of all migratory biota, including shrimp assemblages. Dams without a spillway discharge or any other method to connect the upstream reaches with the downstream ones are known to completely extirpate population of shrimps from all stream reaches located above them by preventing the recruitment of new individuals (Holmquist et al. 1998). Without shrimps, these stream reaches lack the top-down control that regulate the ecosystem properties mentioned above. As a result, streams reaches located above large dams show higher levels of algae, FBOM, sediment, and nutrients compared to streams draining into river without large dams (Greathouse et al. 2006b, Greathouse et al. 2006c).

My dissertation builds on previous studies focusing on the effect of shrimp assemblages on ecosystem-level properties and processes. We use long-term datasets to assess the top-down control by shrimps on benthic resources on large spatial and temporal scales. We also assess the effect of the landscape-scale shrimp extirpations on stream ecosystem processes across the island of Puerto Rico to further understand the extent of how dams can indirectly change the entire stream ecosystem.

CHAPTER 2: Biotic and abiotic controls of algae and fine benthic matter at the reach scale: a long-term comparison of two tropical headwater streams in Puerto Rico

We use established ongoing datasets (10+ years) to describe the importance and variation of shrimp assemblages top-down control on stream benthic resources. Furthermore, we incorporate abiotic variables into our analyses to examine any potential interaction with shrimp top-down control or potential simultaneous effects on benthic resources at the same scales.

CHAPTER 3: Dams reduce leaf litter breakdown rates in tropical headwater streams decades after top migratory consumers extirpation

We assess the effects of shrimp extirpations on the ecosystem processes of organic matter decomposition at the landscape scale. We use a consumer manipulation (exclosure) experiment in a stream reach located above a large dam and a stream without a dam to directly link the presence and absence of shrimp assemblages to litter decomposition rates. We then scale-up and run leaf decomposition experiments in 14 streams reaches (7 located above a large dam and 7 in drainages without a downstream dam) across the island to describe how the presence or absence (through extirpation) of a large dam results in landscape-scale patterns of leaf decomposition rates.

CHAPTER 4: Extirpation of native stream macroconsumers effects on reach-scale nutrient dynamics in tropical headwater streams of Puerto Rico

Following the leaf decomposition experiment, we continue the assessment of shrimp extirpation effects on ecosystem processes at the landscape-scale by focusing on how the presence or absence of shrimp assemblages alter reach-scale nutrient (N and P) dynamics. This study focuses on two aspects: 1) the effects of losing the key functions of the dominant shrimp assemblages, and 2) how these effects change between different seasons. We selected six total stream reaches (3 above a large dam and 3 in drainages without a downstream dam) and ran experimental nutrient addition experiments to estimate uptake length, velocity, and rate of both N and P under both scenarios. All the experiments were done during both the high precipitation and low precipitation season to incorporate the effect of seasonal variation in streamflow.

References

Anderson, E. P., C. M. Pringle, and M. C. Freeman. 2008. Quantifying the extent of river fragmentation by hydropower dams in the Sarapiquí River Basin, Costa Rica. Aquatic Conservation: Marine and Freshwater Ecosystems 18:408-417.

Benstead, J. P., W. F. Cross, J. G. March, W. H. McDowell, A. Ramirez, and A. P. Covich. 2010. Biotic and abiotic controls on the ecosystem significance of consumer excretion in two contrasting tropical streams. Freshwater Biology 55:2047-2061.

Chace, F. A., and H. H. Hobbs. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica [by] Fenner A. Chace, Jr., and Horton H. Hobbs, Jr. Washington, D.C. : Smithsonian Institution Press.

Connelly, S., C. M. Pringle, R. J. Bixby, R. Brenes, M. R. Whiles, K. R. Lips, S. Kilham, and A. D. Huryn. 2008. Changes in Stream Primary Producer Communities

Resulting from Large-Scale Catastrophic Amphibian Declines: Can Small-Scale Experiments Predict Effects of Tadpole Loss? Ecosystems 11:1262-1276.

Covich, A., and W. H. McDowell. 1996. The Stream Community. Pages 434-459 *in* R. B. Waide and W. B. Reagan, editors. The food web of a tropical rainforest. University of Chicago Press, Chicago.

Covich, A. P., M. C. Austen, F. Barlocher, E. Chauvet, B. J. Cardinale, C. L. Biles, P. Inchausti, O. Dangles, M. Solan, M. O. Gessner, B. Statzner, and B. Moss. 2004. The role of Biodiversity in the functioning of freshwater and marine benthic ecosystems. BioScience 54:767-775.

Covich, A. P., T. A. Crowl, C. L. Hein, M. J. Townsend, and W. H. McDowell. 2009. Predator–prey interactions in river networks: comparing shrimp spatial refugia in two drainage basins. Freshwater Biology 54:450-465.

Cross, W. F., A. P. Covich, T. A. Crowl, J. P. Benstead, and A. Ramirez. 2008a. Secondary production, longevity and resource consumption rates of freshwater shrimps in two tropical streams with contrasting geomorphology and food web structure. Freshwater Biology 53:2504-2519.

Cross, W. F., A. Ramírez, A. Santana, and L. Silvestrini Santiago. 2008b. Toward Quantifying the Relative Importance of Invertebrate Consumption and Bioturbation in Puerto Rican Streams. Biotropica 40:477-484.

Crowl, T. A., N. Bouwes, M. J. Townsend, A. P. Covich, and F. N. Scatena. 2001a. Estimating the potential role of freshwater shrimp on an aquatic insect assemblage in a tropical headwater stream: a bioenergetics approach. International

Association of Theoretical and Applied Limnology, Proceedings, Vol 27, Pt 4 27:2403-2407.

Crowl, T. A., W. H. McDowell, A. P. Covich, and S. L. Johnson. 2001b. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82:775-783.

Greathouse, E. A., J. G. March, and C. M. Pringle. 2005. Recovery of a tropical stream after a harvest-related chlorine poisoning event. Freshwater Biology 50:603-615.

Greathouse, E. A., C. M. Pringle, and W. H. McDowell. 2006a. Do small-scale exclosure/enclosure experiments predict the effects of large-scale extirpation of freshwater migratory fauna? Oecologia 149:709-717.

Greathouse, E. A., C. M. Pringle, W. H. McDowell, and J. G. Holmquist. 2006b. Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico. Ecol Appl 16:339-352.

Hein, C. L., A. S. Pike, J. F. Blanco, A. P. Covich, F. N. Scatena, C. P. Hawkins, and T. A. Crowl. 2011. Effects of coupled natural and anthropogenic factors on the community structure of diadromous fish and shrimp species in tropical island streams. Freshwater Biology 56:1002-1015.

Holmquist, J. G., J. M. Schmidt-Gengenbach, and B. B. Yoshioka. 1998. High dams and marine-freshwater linkages: Effects on native and introduced fauna in the Caribbean. Conservation Biology 12:621-630.

March, J. G., J. P. Benstead, C. M. Pringle, and M. W. Ruebel. 2001. Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. Canadian Journal of Fisheries & Aquatic Sciences 58:470.

March, J. G., C. M. Pringle, M. J. Townsend, and A. I. Wilson. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. Freshwater Biology 47:377-390.

Pringle, C. M. 1996. Atyid shrimps (Decapoda: Atyidae) influence the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. Freshwater Biology 35:125.

Pringle, C. M., and G. A. Blake. 1994. Quantitative Effects of Atyid Shrimp (Decapoda, Atyidae) on the Depositional Environment in a Tropical Stream - Use of Electricity for Experimental Exclusion. Canadian Journal of Fisheries and Aquatic Sciences 51:1443-1450.

Pringle, C. M., G. A. Blake, A. P. Covich, K. M. Buzby, and A. Finley. 1993. Effects of Omnivorous Shrimp in a Montane Tropical Stream - Sediment Removal, Disturbance of Sessile Invertebrates and Enhancement of Understory Algal Biomass. Oecologia 93:1-11.

Pringle, C. M., and T. Hamazaki. 1997. Effects of fishes on algal response to storms in a tropical stream. Ecology 78:2432-2442.

Pringle, C. M., N. Hemphill, W. H. McDowell, A. Bednarek, and J. G. March. 1999. Linking species and ecosystems: Different biotic assemblages cause interstream differences in organic matter. Ecology 80:1860-1872.

Ramirez, A., and L. R. Hernandez-Cruz. 2004. Aquatic insect assemblages in shrimp-dominated tropical streams, Puerto Rico. Biotropica 36:259-266.

Ranvestel, A. W., K. R. Lips, C. M. Pringle, M. R. Whiles, and R. J. Bixby. 2004. Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. Freshwater Biology 49:274-285.

Smith, G. C., A. P. Covich, and A. M. D. Brasher. 2003. An Ecological Perspective on the Biodiversity of Tropical Island Streams. Pages 1048-1051 BioScience.

Taylor, B. W., A. S. Flecker, and R. O. Hall, Jr. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science 313:833-836.

Vaughn, C. C. 2010. Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging Conclusions and Research Directions. BioScience 60:25-35.

Whiles, M. R., R. O. Hall, W. K. Dodds, P. Verburg, A. D. Huryn, C. M. Pringle, K. R. Lips, S. S. Kilham, C. Colon-Gaud, A. T. Rugenski, S. Peterson, and S. Connelly. 2013. Disease-Driven Amphibian Declines Alter Ecosystem Processes in a Tropical Stream. Ecosystems 16:146-157.

Wright, M. S., and A. P. Covich. 2005. The Effect of Macroinvertebrate Exclusion on Leaf Breakdown Rates in a Tropical Headwater Stream. Biotropica 37:403-408.

CHAPTER 2

BIOTIC AND ABIOTIC CONTROLS OF ALGAE AND FINE BENTHIC MATTER AT THE REACH SCALE: A LONG-TERM COMPARISON OF TWO TROPICAL HEADWATER STREAMS IN PUERTO RICO[1]

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[1] P. J. Torres, O. Perez-Reyes, A.S. Mehring, E.A. Greathouse, K.L. Smith, A.P. Covich, T.A. Crowl, W.H. McDowell, A.Ramírez, and C.M. Pringle. To be submitted to *Ecosystems*

Abstract

Consumers are an integral part of ecosystems due to their top-down effects on food resources which, in turn, affect other ecosystem properties and processes. Here we present a 10-year (2002-2012) dataset of algae, benthic organic matter, benthic inorganic-matter, shrimp macroconsumers, and chemical and physical variables from two different headwater stream reaches (~ 1 km), one with high densities of native shrimps (Prieta; > 20 individuals m^{-2}) and another with significantly lower densities (Bisley <3 individuals m^{-2}). Analysis of the entire survey period shows twice as much chlorophyll-a, 9-fold more organic matter, and 21-fold more inorganic-matter were measured in Bisley (5858µg cholophyll-a m^{-2}, 28.7g AFDM m^{-2}, 6.7g inorganic-matter m^{-2}) than in Prieta (2510µg cholophyll-a m^{-2}, 3.1g AFDM m^{-2}, 6.7g inorganic-matter m^{-2}). There is no top-down control regulation of algal standing crop and other benthic resources in Bisley. In contrast, the constant and significantly lower levels for all benthic resources measured and their virtually non-existent spatial temporal variability in Prieta seems to be directly associated by strong top-down control by shrimps.

Introduction

Ecosystem properties and processes are regulated by both biotic and abiotic factors, but the relative importance of one over the other can be context dependent. For example, grazers can regulate the total biomass of primary producers though their feeding and therefore manipulate the overall net primary production of a system (Frank et al. 2002). Consumer community composition or fluctuating densities then can have significant effects on ecosystem processes. On the other hand, abiotic factors such as light and nutrient availability may have similar effects depending on the system (Hill and Knight 1988). Biotic and abiotic variables usually can influence the same aspect of the system but the magnitude at which they influence the ecosystem properties or processes rate and their relative importance may change in space and time (Rosemond et al. 2000).

In stream ecosystems, physical changes in the channel are often followed by changes in the overall habitat, community structure, and food resources available to the stream community (Vannote et al. 1980). Stream basal food resources include coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), benthic organic matter (FBOM), and algae. The availability of CPOM is often linked to direct allochthonous inputs and upstream transport, but the amount of smaller benthic food resources (FBOM and algae) is more associated processes within the stream, particularly the consumer community structure and their activity (Tank et al. 2010). For example, the presence of shredders and their community composition determine the decomposition rates of CPOM and its reduction into FPOM (Wallace and Webster 1996, Wantzen et al. 2008). This transformation results in smaller organic matter particles floating in the water column available for other consumers (e.g. filter feeders, gatherers), and more organic particles getting deposited on the streambed to increase the levels of FBOM. Furthermore, grazers feeding on algae are known to increase overall primary production in the benthic habitat by preventing saturation and increasing turnover rates (Lamberti and Resh 1983).

In Puerto Rico, the consumer communities in high elevation streams are dominated by freshwater shrimps assemblages (Pringle et al. 1993, Covich and McDowell 1996). There are 17 species of freshwater shrimps from three different families within the island (Xiphocarididae, Atyidae, and Palaemonidae) and all three families are usually represented in high elevation streams draining free-flowing watersheds (Perez-Reyes et al. 2013). Shrimps assemblages are usually found in high abundances (>20 individuals m^{-2}) and often represent the majority of the consumer assemblage total biomass (Covich and McDowell 1996, Covich et al. 1996). Shrimps are active feeders and different species can employ different feeding mechanisms (e.g. collecting, filtering) to obtain their food. Besides feeding, they also remove and re-suspend significant amounts of inorganic sediments through bioturbation (Pringle et al. 1993, Cross et al. 2008). This combination of diverse feeding mechanisms coupled with their dominant presence makes them an integral piece for maintaining ecosystem function in Puerto Rican streams.

Many studies have assessed the strong top–down control of shrimp assemblages on benthic food resources and sediments in Puerto Rico. These studies have shown different scenarios in which basal food resources (FBOM or algae) levels are significantly higher due to the absence of shrimps. For example: (1) when shrimps are experimentally excluded from small (< 1m^{-2}) areas of rock substrate within a stream reach (Pringle et al. 1993, Pringle and Blake 1994, Pringle 1996, Pringle et al. 1999, Greathouse et al. 2006a), (2) when all shrimps within a stream reach are killed by an isolated poisoning event (Greathouse et al. 2005), (3) in low elevation streams reaches where their abundance is lower due to the presence of fish predators (March et al. 2002), and (4) in reaches where they have been completely extirpated for decades by an in-channel large dam that prevents them from migrating upstream (Greathouse et al. 2006b). In these cases, the elevated levels of either algae or FBOM were directly to the lack or reduced top-down control linked to the absence or substantial density reduction of shrimps. However, the landscape and long-term extent of how this strong top-down control by shrimps affect benthic resources at broader spatial and temporal scales is still unknown (but see Greathouse et al. 2006). There is also little information on how abiotic factors affect basal food resources when shrimps are found in low densities or when they are absent, and whether or not these can replace the role of shrimps in streams where the latter are absent or found in very low densities.

My goal in this study is to characterize both intra- and inter- stream variability of benthic food resources (algae and fine benthic organic matter) and inorganic sediments using over 10 years of continuous monitoring data to address the following question: To what degree do shrimps top-down control regulate benthic resources temporally (10 yrs period) and spatially (1 km stream reach). We use long-term established datasets to contrast a stream reach with naturally occurring low-shrimp densities (< 1 individual m^{-2}) against a nearby representative stream reach with high shrimp density (>25 individuals m^{-2}) and biomass. I predict that in the high shrimp density stream, their assemblage will exert a strong and constant top-down control on algae, FBOM and inorganic sediments, maintaining them at significantly lower levels that in the shrimp-poor stream over the entire reach (1km) and for the entire ten-year period. However, in the shrimp-poor stream, we expect the lack of strong top-down control to result in a significantly higher range of variability in these parameters (relative to the shrimp-abundant stream) resulting in high intra-stream variation and patchiness in benthic resources over the entire ten-year period. We also expect abiotic variables to have a higher influence on benthic resources in the shrimp-poor stream where top-down control is virtually non-existent.

Methods

Study sites

I used data available from two focal streams located within El Yunque National Forest (EYNF) in the Northeast region of Puerto Rico. El Yunque is the only tropical rainforest under protection and management by the United States Agriculture Department Forest Service (USDA FS). This region receives an annual average precipitation of 3500mm with a subtle seasonal variation resulting in less frequent storm events and lower average discharge between January and April (Larsen 2000). In one of the streams, Prieta, shrimps densities are high (around 33 individuals m^{-2}) due to the presence of a steep waterfall downstream from our study reaches. Waterfalls are known to prevent the upstream migration of shrimp predators (i.e. predatory fish) resulting in refuge zones for shrimps (Covich et al. 2009). Our second study stream, Bisley, drains a lower gradient watershed without any steep water drops. Predatory fishes can swim freely upstream of our study reach keeping the shrimp assemblage at extremely low numbers (<1 individual m^{-2}). Both streams have similar physical and chemical characteristics with the exception of nitrates and phosphates being slightly higher in Bisley (Table 2.1).

I synthetized data available from the Luquillo Long-Term Ecological Research site (LUQ-LTER) long-term data bases on stream benthic resources (algae, FBOM, and FBIM; database #136), shrimp assemblages (database #54), and water chemistry (database #20). All data were available for both Bisley and Prieta streams. Data were collected at various interval since the establishment of the project in 1988. For this study we focused on the 2002 – 2013 period. Below are the descriptions of the sampling protocol and frequency for all variables.

Benthic algae, benthic organic matter, and inorganic sediments

Algae and benthic material samples were collected from six pre-established monitoring pools in each streams (n= 6 per stream). Samples were collected twice every year (Once in the high rain season and once in the low rain season). At each pool (n=6) we collected a composite sample of six sub samples taken using a suction device modified from Loeb (1981) with a sampling area of 0.0029 m-2. In 2005, three sampling pools from Prieta and four sampling pools from Bisley were eliminated and replaced with new sampling pools to match the ones being used to monitor shrimp populations (description below). Samples were collected directly from rocks and boulders submerged at least 30cm into the pool. Each sample was stored in ice, transported to the lab and processed within the next 48hours. For processing, samples were split into two subsamples and filtered into a pre-combusted glass fiber filters (Whatman GF/F pore size 0.7 µm). One filter was used to estimate algae levels by extracting chlorophyll a (chl a) and calculating its concentration using the fluorometric method described by APHA (2005). The second filter was dried at 65° C for 24 hours, weighed, and then ashed at 500° C for one hour and reweighed to estimate fine benthic organic matter (FBOM) and fine benthic inorganic matter (FBIM) by calculating the total ash-free dry mass (AFDM).

Shrimp assemblages

Shrimp populations have been monitored from the same 6 pools in our two study streams since 1989. For this study we only used the period of data that matched our algae and benthic material sampling period (Summer 2002 – Spring 2013). Shrimp surveys were also conducted twice a year (once in the high rain season and once in the low rain season). Baited minnow traps (mesh size = 0.40 cm-2) were deployed at a density of 0.5 traps m-2 in each of the sampling pools during the afternoon and retrieved the next morning (Covich et al. 1991). All shrimps collected within each trap were counted, identified, and released back into the pool. For our analysis, we only considered density and abundance from two genus, *Xiphocaris* and *Atya*, and Total shrimp abundance (the sum of both genus (*Xiphocatis* + *Atya*). Abundance value were transformed into densities using the surface are of the pool sampled. We focused on *Xiphocaris* and *Atya* genus because they represent ~90% of the catch. Also, these are the two taxa are a good representation of all feeding groups within the overall assemblage. Thus, they have a significant effect on benthic food resources based on previous studies

Water physicochemical properties and streamflow

Water samples were collected weekly from a single pool in each of our study streams. A single sample is collected at one central location within our study reach and frozen within the next 6 hours until processing. Each sample is analyzed for pH, Conductivity, NO_3^-, NH_4^+, PO_4^{3-}, total dissolved nitrogen (TDN), and total suspended solids (TSS). Streamflow is constantly monitored at each stream using in situ pressure loggers. Mean daily discharge was estimated from hourly measurements. Additional discharge values for the analysis were generated by adding daily discharge values over a determined period before the date of interest (Table 2.2). We also calculated days since the last storm as a model variable with storm events determined as the days in which the average daily discharge was higher than the annual average plus it's standard deviation.

Statistical Analyses

We used two-ways ANOVAs to test for overall intra- and inter-stream differences in benthic resources between Bisley and Prieta and during both the high rain and the low rain season. Chlorophyll a, FBOM, and FBIM values were log-transformed to correct for normality over the 10 years period. We used linear regression to test for correlation between pool location and all benthic parameters measured within each stream before pooling each independent pool into the multiple regression models. We used multiple regressions models to estimate the effects of shrimps and abiotic factors on the three benthic resources measured. All potential models were then ranked with Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson 2003). All variables considered in the models ranked by AIC are listed in Table 2.2. Only the models with $\Delta i < 2$ were selected as the best candidates since these provide substantial evidence for the parameter effects on Chl *a*, FBOM, and FBIM. The y-intercept was included as a model parameter.

Results

There was no significant relationship between pool location and any of the three benthic resources measured for neither Prieta ($p < 0.001$) nor Bisley ($p<0.001$) over the entire sampling period (Figure 2.1). Mean values (10 yrs) of all three benthic resources measured in the entire sampling reach (1km) were significantly higher in Bisley than in Prieta during both the high rain ($p<0.001$ for all three) and the low rain seasons ($p<0.001$ for all three; Figure 2.3). Intra stream seasonal variation was only significant for Chl *a* in Prieta ($p<0.0032$). There was no significant difference in mean benthic resource levels for any of the three parameters measured between the high rain and low rain seasons in Bisley ($p > 0.1$).

Chlorophyll *a* was best predicted by *Xiphocaris* and NO_3. The parameter estimate from each independent variable suggest that *Xiphocaris* have a negative effect on the Chlorophyll *a* levels. For NO_3 the estimate is very low but it was positive, suggesting a positive relationship between NO_3 in the water and benthic algae (Table 2.3). Fine benthic organic matter (FBOM) was best explained by three different models, (1) *Atya*, (2)*Xiphocaris*, and (3) *Atya* and Season. Shrimps were the overall dominant factor regulating FBOM based on the best models selected by the analysis. The combination of Atya and season was also selected as one of the significant models (Table 2.3). Fine benthic inorganic matter (FBIM) was best explained by four different models, (1) Total shrimp density, (2) Total shrimp density and season,(3) *Atya*, and (4) *Atya* and Total suspended solids. There were no abiotic factor-only models selected by the AIC for neither of the three benthic resource considered.

Discussion

My results reaffirm the essential role of shrimps in regulating benthic resources in high elevation streams in Puerto Rico. The high variability in Bisley for all benthic parameters measured (Chl *a*, FBOM, FBIM) can be attributed to the virtual lack of top-down control due to extremely low shrimp abundances (< 1 individual m^{-2}). This line of evidence is supported by previous studies that experimentally reduced or completely excluded shrimp assemblages resulting in estimates similar to the values we got for Bisley (Pringle and Blake 1994, Pringle et al. 1999, March et al. 2002, Greathouse et al. 2005). All the candidate models selected by the AIC for all the benthic parameters considered included at least one of the shrimp variables, suggesting that even under very low densities the abiotic factors are not enough to compensate for the lack of a strong top-down control to keep the benthic resource levels low. Each candidate model included at least one shrimp assemblage parameter. In Prieta, the low-level and low-variability pattern was persistent year to year for the entire period considered (2002 – 2013; Figure 2.2).

Contrary to our expectations, none of the abiotic variables considered came out as a standalone factor regulating benthic resources. Neither discharge, nor days since last storm have a significant effect on and of the benthic parameters measured. We expected for this abiotic factor to compensate for the lack of top-down control in Bisley based on previous studies finding discharge as a vector to scour algae and benthic material during high flow events (Pringle and Hamazaki 1997). As part of our sampling protocol for benthic resources, all samples were collected at least three days since the last rain event to keep the sampling standardized over the years. It is possible that three days were enough for the benthic parameters to return to normal levels between any significant rain event and out sampling date (Stevenson 1990, Peterson et al. 1994). In order to better assess the influence of abiotic factors on benthic food resources and inorganic sediments a more frequent sampling of these parameters that include precipitation high discharge events may be needed. Another possibility is the fact that since FBOM and FBIM levels are so low in Prieta, any removal by increased discharge events might go unnoticeable. Season was one of the significant variables in selected models explaining FBOM and FBIM, although the parameter importance weight estimate was always lower than the shrimp parameters included in the same model. Also, benthic parameters seasonal mean levels for the whole reach were not significantly different between seasons for any of the streams (Figure 2.3). This suggest either a very subtle synergy between seasonal variation and shrimp assemblages, or potential intra stream variation (not considered independently within the model) driven by seasonal changes. Once again, the *snapshot* sampling protocol is limiting our ability to detect regulation by abiotic factors or significant synergies between them and top-down control by shrimps.

The significant difference between Bisley and Prieta for all benthic parameters across both the low-rain and high-rain seasons also highlights the landscape influence on in-stream processes because of the difference in shrimp densities between the two streams. In the Prieta stream, low levels and low intra-stream variability in all three benthic parameters (chlorophyll a, FBOM, and FBIM) reflect strong and constant top-down control by shrimp assemblages along a 1 km reach. The indirect effect of the waterfall located downstream of the sampling reach in Prieta is the origin for the difference in community assemblage composition (Covich et al. 2009, Hein et al. 2011). Although shrimp top-down control seems to be the driving force regulating benthic resources above waterfalls, all the effect is lost downstream in higher order streams with lower gradients where shrimp predators are abundant (March et al. 2001, March et al.

2002). Thus, this localized effect remains exclusive to low-order and high elevation streams. In contrast, in the Bisley stream, significantly higher levels of all three response variables and higher intra-stream variability than Prieta. In streams of the EYNF, strong top-down control occurs in headwater streams above waterfalls where shrimps reach high abundance in the absence of fish predators (Prieta) and low top-down control occurs in headwater streams with no waterfalls (Bisley) where shrimp densities are low due to fish predation. Our study highlights how landscape features can indirectly influence significant ecosystem properties within the stream habitats. This long-term dataset is critical to establishing how natural assemblages of native stream organisms structure stream ecosystems.

References

APHA. 2005. Standard methods for the examination of water and wastewater. Washington, DC.

Burnham, K. P., and D. R. Anderson. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Covich, A., and W. H. McDowell. 1996. The Stream Community. Pages 434-459 *in* R. B. Waide and W. B. Reagan, editors. The food web of a tropical rainforest. University of Chicago Press, Chicago.

Covich, A. P., T. A. Crowl, C. L. Hein, M. J. Townsend, and W. H. McDowell. 2009. Predator–prey interactions in river networks: comparing shrimp spatial refugia in two drainage basins. Freshwater Biology 54:450-465.

Covich, A. P., T. A. Crowl, S. L. Johnson, and M. Pyron. 1996. Distribution and abundance of tropical freshwater shrimp along a stream corridor: Response to disturbance. Biotropica 28:484-492.

Covich, A. P., T. A. Crowl, S. L. Johnson, D. Varza, and D. L. Certain. 1991. Post-Hurricane Hugo Increases in Atyid Shrimp Abundances in a Puerto-Rican Montane Stream. Biotropica 23:448-454.

Cross, W. F., A. Ramírez, A. Santana, and L. Silvestrini Santiago. 2008. Toward Quantifying the Relative Importance of Invertebrate Consumption and Bioturbation in Puerto Rican Streams. Biotropica 40:477-484.

Frank, D. A., M. M. Kuns, and D. R. Guido. 2002. Consumer control of grassland plant production. Ecology 83:602-606.

Greathouse, E. A., J. G. March, and C. M. Pringle. 2005. Recovery of a tropical stream after a harvest-related chlorine poisoning event. Freshwater Biology 50:603-615.

Greathouse, E. A., C. M. Pringle, and W. H. McDowell. 2006a. Do small-scale exclosure/enclosure experiments predict the effects of large-scale extirpation of freshwater migratory fauna? Oecologia 149:709-717.

Greathouse, E. A., C. M. Pringle, W. H. McDowell, and J. G. Holmquist. 2006b. Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico. Ecol Appl 16:339-352.

Hein, C. L., A. S. Pike, J. F. Blanco, A. P. Covich, F. N. Scatena, C. P. Hawkins, and T. A. Crowl. 2011. Effects of coupled natural and anthropogenic factors on the community structure of diadromous fish and shrimp species in tropical island streams. Freshwater Biology 56:1002-1015.

Hill, W. R., and A. W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams. Journal of Phycology 24:125-132.

Lamberti, G. A., and V. H. Resh. 1983. Stream Periphyton and Insect Herbivores: An Experimental Study of Grazing by a Caddisfly Population. Page 1124. The Ecological Society of America.

Larsen, M. C. 2000. Analysis of 20th century rainfall and streamflow to characterize drought and water resources in Puerto Rico. Physical Geography 21:494-521.

Loeb, S. L. 1981. An in situ method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. Limnology and Oceanography 26:394-399.

March, J. G., J. P. Benstead, C. M. Pringle, and M. W. Ruebel. 2001. Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. Canadian Journal of Fisheries & Aquatic Sciences 58:470.

March, J. G., C. M. Pringle, M. J. Townsend, and A. I. Wilson. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. Freshwater Biology 47:377-390.

Perez-Reyes, O., T. A. Crowl, P. J. Hernandez-Garcia, R. Ledesma-Fuste, F. A. Villar-Fornes, and A. P. Covich. 2013. Freshwater decapods of Puerto Rico: a checklist and reports of new localities. Zootaxa 3717:329-344.

Peterson, C. G., A. C. Weibel, N. B. Grimm, and S. G. Fisher. 1994. Mechanisms of benthic algal recovery following spates: comparison of simulated and natural events. Oecologia 98:280-290.

Pringle, C. M. 1996. Atyid shrimps (Decapoda: Atyidae) influence the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. Freshwater Biology 35:125.

Pringle, C. M., and G. A. Blake. 1994. Quantitative Effects of Atyid Shrimp (Decapoda, Atyidae) on the Depositional Environment in a Tropical Stream - Use of Electricity for Experimental Exclusion. Canadian Journal of Fisheries and Aquatic Sciences 51:1443-1450.

Pringle, C. M., G. A. Blake, A. P. Covich, K. M. Buzby, and A. Finley. 1993. Effects of Omnivorous Shrimp in a Montane Tropical Stream - Sediment Removal, Disturbance of Sessile Invertebrates and Enhancement of Understory Algal Biomass. Oecologia 93:1-11.

Pringle, C. M., and T. Hamazaki. 1997. Effects of fishes on algal response to storms in a tropical stream. Ecology 78:2432-2442.

Pringle, C. M., N. Hemphill, W. H. McDowell, A. Bednarek, and J. G. March. 1999. Linking species and ecosystems: Different biotic assemblages cause interstream differences in organic matter. Ecology 80:1860-1872.

Rosemond, A. D. 1994. Multiple Factors Limit Seasonal-Variation in Periphyton in a Forest Stream. Journal of the North American Benthological Society 13:333-344.

Rosemond, A. D., P. J. Mulholland, and S. H. Brawley. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. Canadian Journal of Fisheries and Aquatic Sciences 57:66-75.

Stevenson, R. J. 1990. Benthic algal community dynamics in a stream during and after a spate. Journal of the North American Benthological Society 9:277-288.

Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entrekin, and M. L. Stephen. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29:118-146.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual review of entomology 41:115-139.

Wantzen, K. M., C. M. Yule, J. M. Mathooko, and C. M. Pringle. 2008. Organic Matter Processing in Tropical Streams. Tropical Stream Ecology:43-64.

Tables

Table 2.1: Physicochemical characteristics and densities of the most dominant shrimp taxa (*Xiphocaris elongata* and *Atya spp.*) within the long-term (2002-2013) monitoring reaches of two headwaters streams (Bisley and Prieta) at El Yunque National Forest, Puerto Rico. All values presented as mean ± 1SE (*N*).

Parameter	Sampling frequency	Study stream							
		Bisley				Prieta			
		value		SE	(N)	value		SE	(N)
Xiphocaris elongata density (# individuals m^{-2})	Biannually	0.18	±	0.03	(124)	16.06	±	2.21	(124)
Atya spp. density (# individuals m^{-2})	Biannually	0.001	±	0.001	(124)	16.73	±	2.49	(124)
Discharge (L s^{-1})	Daily	28.03	±	0.78	(2964)	27.06	±	1.55	(1196)
Pool width (m)	Biannually	4.10	±	0.08	(336)	2.56	±	0.07	(360)
Pool depth (m)	Biannually	0.46	±	0.01	(565)	0.35	±	0.01	(565)
NO_3-N (µgN L^{-1})	Weekly	96.51	±	2.08	(421)	57.49	±	1.31	(424)
NH_4-N (µgN L^{-1})	Weekly	4.88	±	0.29	(420)	6.46	±	0.49	(422)
PO_4^{3-} (µgP L^{-1})	Weekly	12.47	±	0.32	(415)	4.52	±	0.20	(413)
TSS (mg L^{-1})	Weekly	5.69	±	0.36	(418)	8.57	±	0.46	(418)

Table 2.2: All variables considered in the initial Multiple Regression analyses prior to the AIC model selections.

Variable	**Actual values considered in initial analysis**
Atya spp. (individuals m^{-2}), *Xiphocaris elongata* (individuals m^{-2})	Mean number by pool; split by season (High rain, low rain)*
Total shrimp (individuals m^{-2})	*Atya spp. + Xiphocaris elongata* Mean number by pool; split by season (High rain, low rain)*
Season (High rain, low rain)	Benthic parameters and shrimp measurements were classified based on the date they were collected (High rain = May-December; Low rain = Jan-April)
Discharge (L s^{-1})	Daily mean for sampling date Daily mean for sampling date plus daily mean for the last 3 days Daily mean for sampling date plus daily mean for the last 5 days Daily mean for sampling date plus daily mean for the last 10 days
Days since last storm (days)	DSLS**
pH, Conductivity (mS m^{-1}), NO3 (µgN L^{-1}), NH4 (µg L^{-1}), PO4 (µP L^{-1}), TDN (mg L^{-1}), TSS (mg/L)	Closest value to actual sampling date*** Mean for the last 2 weeks of the closest value to the sampling date Mean for the last 3 weeks of the closest value to the sampling date

*Estimated from the same sampling pools, collected during the same seasons but not during the same date

** Storms were defined as the days when the average daily discharge was higher than the daily average plus the standard deviation for the year.

*** Physicochemical variables were sampled once a week during the 11-year period.

Table 2.3: Top candidate models, from Akaike's Information Criterion (AICc) scores, explaining algal standing crop, fine benthic organic matter, and fine benthic inorganic matter in both streams. The best candidate models for each variable are highlighted in **bold**. Only the models with $\Delta_i < 2$ were selected as the best candidate since these provide substantial evidence for the parameter effects on Chl *a*, FBOM, and FBIM (Burnham and Anderson 2002). The y-intercept was included as a model parameter.

	K	C_p	R^2_{adj}	AICc	Δ_i	*L*	w_i
A) Chl *a*							
NO$_3$, *Xiphocaris*	**4**	**0.34**	**0.56**	**-64.84**	**0**	**1**	**0.70**
NO$_3$, NH$_4$, *Xiphocaris **	5	1.57	0.56	-63.11	1.73	0.42	0.30
pH, NO$_3$, *Xiphocaris*	5	1.96	0.56	-62.65	2.19	0.33	0.24
Season, NO$_3$, *Xiphocaris*	5	2.23	0.55	-62.34	2.50	0.29	0.20
NO$_3$, PO$_4$, *Xiphocaris*	5	2.32	0.55	-62.23	2.62	0.27	0.19

Parameter:	***Xiphocaris***	**NO$_3$**
Parameter estimate:	-0.035	0.007

	K	C_p	R^2_{adj}	AICc	Δ_i	*L*	w_i
B) FBOM							
Atya	**3**	**0.61**	**0.70**	**-35.10**	**0**	**1**	**0.45**
Xiphocaris	**3**	**1.52**	**0.69**	**-34.12**	**0.98**	**0.61**	**0.28**
***Atya,* Season**	**4**	**1.29**	**0.70**	**-34.12**	**0.98**	**0.61**	**0.28**
Atya, *Xiphocaris*	4	2.27	0.70	-33.03	2.07	0.35	0.16
Atya, Total shrimp density	4	2.57	0.69	-32.71	2.39	0.30	0.14

Parameter:	***Atya***	***Xiphocaris***	**Season**
Parameter importance weigh**:	0.73	0.28	0.28

	K	C_p	R^2_{adj}	AICc	Δ_i	*L*	w_i
C) FBIM							
Total shrimp density	**3**	**2.80**	**0.86**	**-30.74**	**0**	**1**	**0.38**
Total shrimp density, Season	**4**	**3.08**	**0.86**	**-30.01**	**0.73**	**0.70**	**0.26**
Atya	**3**	**3.90**	**0.85**	**-29.63**	**1.11**	**0.57**	**0.22**
***Atya*, TSS**	**4**	**4.15**	**0.86**	**-28.85**	**1.88**	**0.39**	**0.15**
Atya + *Xiphocaris*, TSS	4	4.39	0.85	-28.86	2.13	0.35	0.13

Parameter:	***Atya + Xiphocaris***	***Atya***	**Season**	**TSS**
Parameter importance weigh**:	0.64	0.36	0.26	0.15

**The second top model for Chl a met the AIC requirement for selection as one of the best models. However we do not include it because NH$_4$ was not statistically significant ($p=0.37$) as a parameter predicting an effect on Chl a, and its parameter estimate (0.16) was lower than its standard error (0.18).*

***Parameter importance weighs are calculated only for the selected best models.*

Figures

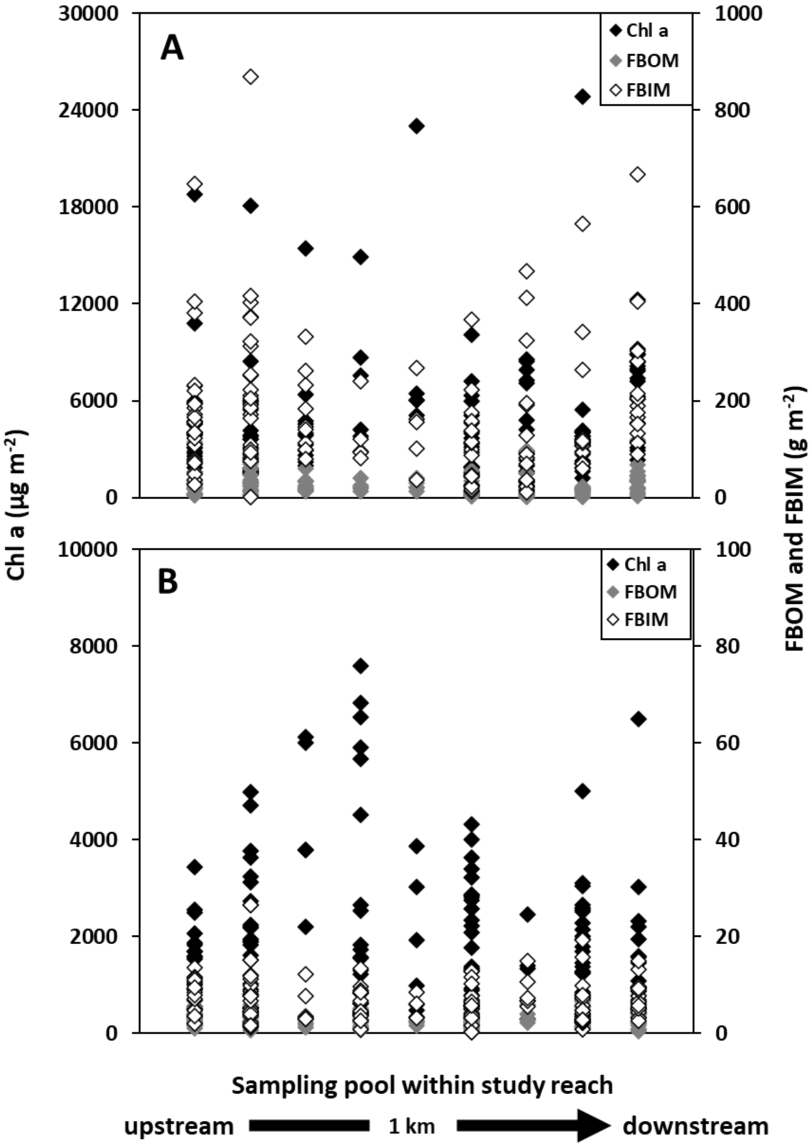

Figure 2.1: Linear Regressions between sampling pool location and all benthic parameters measured at Bisley (A), and Prieta (B). All relationships were not significant ($P > 0.1$, $R^2 \leq 0.01$)

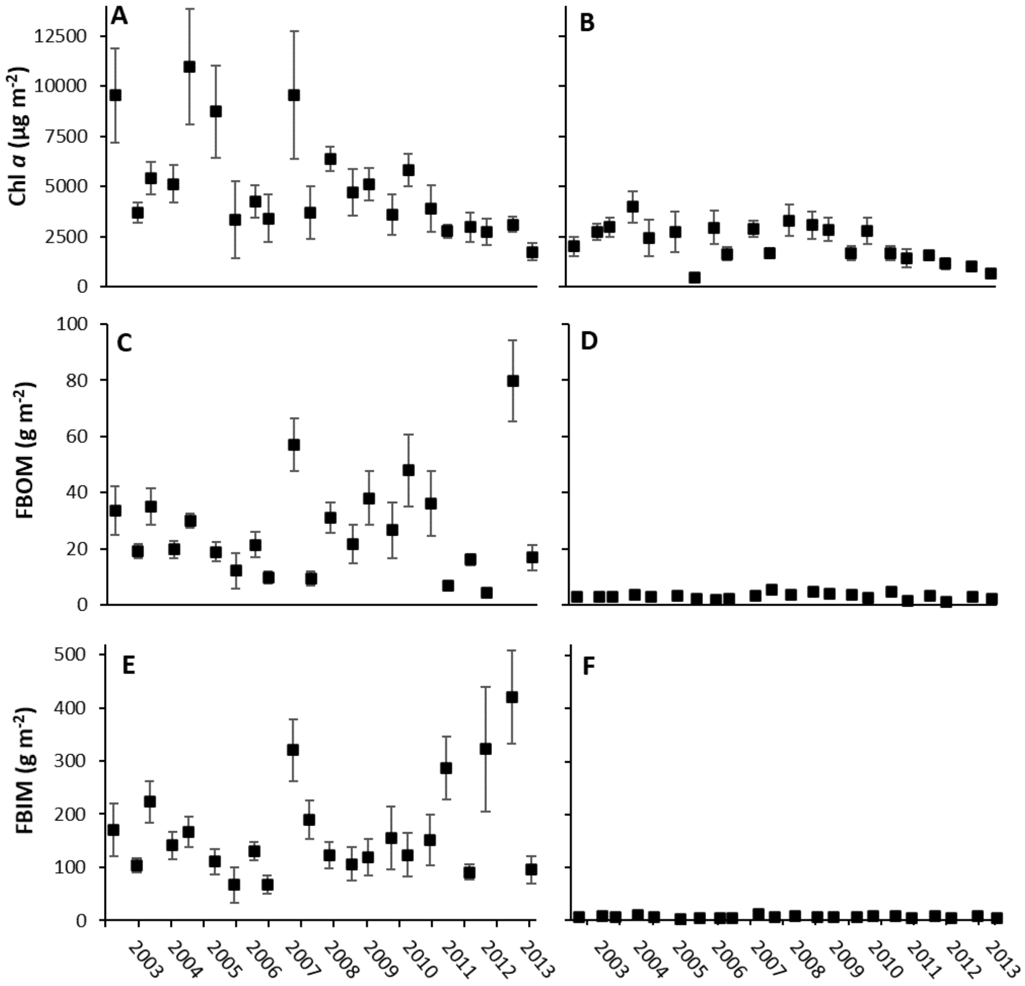

Figure 2.2: Long-term levels (mean ± 1SE) of chlorophyll *a* (Chl *a*), fine benthic organic matter (FBOM), and fine benthic inorganic matter (FBIM) over the 11-year sampling period for Bisley (low shrimp density, A,C,E) and Prieta (high shrimp density, B,D,F).

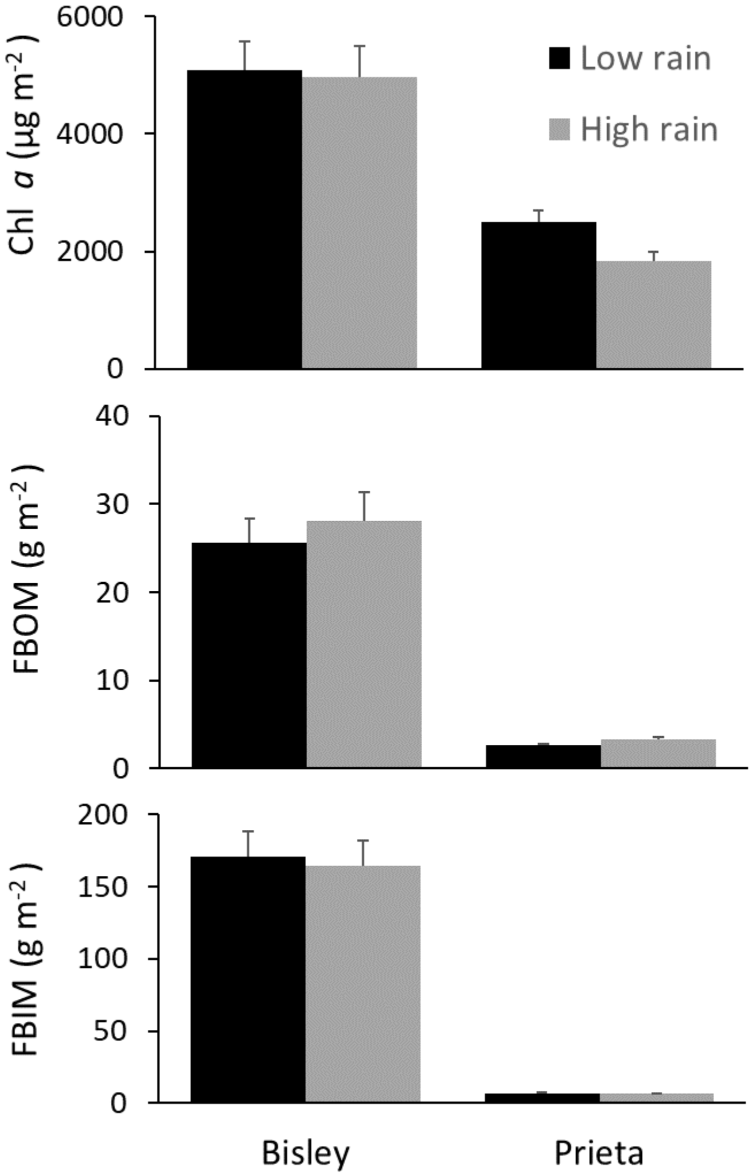

Figure 2.3: Ten-year mean (+ 1SE) of benthic chlorophyll *a* (Chl *a*), fine benthic organic matter (FBOM), and fine benthic inorganic matter (FBIM) for both study streams Bisley and Prieta. Samples were collected biannually once during the low rain season (January-April) and once during the high rain season (May-December).

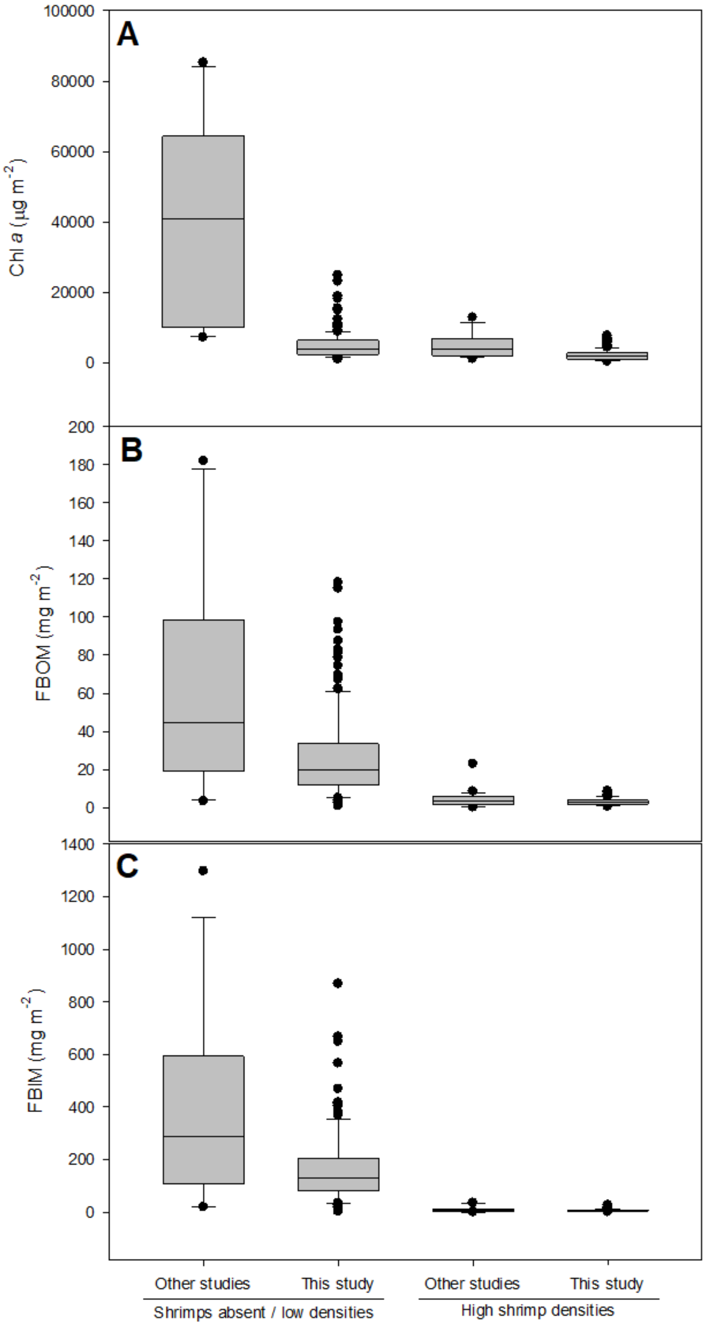

Figure 2.4. Levels of (A) chlorophyll *a*, (B) fine benthic organic matter [FBOM], and (C) fine benthic inorganic matter [FBIM] for our study and other published values for Puerto Rican streams with contrasting shrimp densities. The grey box ranges from the 24th to the 75th percentile, the black line across each box is the median and the error bars are the 9th and 10th percentile. All the black circles are outliers within each category.

CHAPTER 3

DAMS REDUCE LEAF LITTER BREAKDOWN RATES IN TROPICAL HEADWATER STREAMS DECADES AFTER TOP MIGRATORY CONSUMERS EXTIRPATION[1]

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[1] Torres P.J. and C.M. Pringle. To be submitted to *Ecological Applications*

Abstract

Large dams that completely block access of native migratory biota to upstream headwater reaches over decades provide an opportunity to examine effects of long-term biotic extirpation on ecosystem processes and to examine if other organisms have since provided functional redundancy. The relatively high density of large dams across the island of Puerto Rico provide a template to examine how dams affect ecosystem processes at landscape scales. Streams of Puerto Rico are dominated by migratory fishes and shrimps which have been extirpated from headwater stream reaches upstream of large dams, many constructed decades ago. Previous studies in relatively free-flowing rivers in Puerto Rico have shown that shrimps play a key role in the process of decomposition, significantly enhancing leaf decomposition rates. Here, we use experimental *in situ* manipulations of shrimp presence and absence to assess their direct effect on leaf decomposition rates in a headwater stream reach upstream of a large dam (*dammed*) and in a free-flowing undammed stream reach. We then conducted a landscape-scale study where we measured leaf decomposition rates over x days within multiple other dammed (n=7) and undammed (n=7) streams across the island of Puerto Rico. Free-flowing undammed streams inhabited by native shrimp macroconsumers had significantly ($P<0.05$) greater rates of leaf decomposition than stream reaches above dams where shrimps have been absent for decades.

Introduction

Freshwater species are experiencing losses at higher rates than their terrestrial counterparts (Master et al. 2000, Dudgeon et al. 2006, Strayer and Dudgeon 2010). The ecosystem-level effects of losing species in freshwater systems is directly linked to either the functional role of the species, or their dominance within the community (Pringle and Hamazaki 1998, (Covich et al. 2004, Vaughn 2010). A general decline in freshwater biodiversity does not always result in a negative effect on ecosystem function (Creed et al. 2009). However, the loss of species that play a key functional role (e.g. ecosystem engineers) can have strong ecosystem-level consequences, especially when there are no other functionally redundant species in the same system. Species that play key functional roles in streams are often lost or dramatically reduced in abundance before their ecosystem-level effects have been acknowledged, yet alone quantified. As just one example, once zebra mussels became established in the Hudson River (NY, USA), the whole ecosystem structure and function changed but it was not possible to distinguish between the effects of the invasion to the effect of the loss of the native species (Strayer et al. 1999).

Less developed landscapes in developing countries, with river networks under lower anthropogenic stress, present an opportunity to quantify ecosystem- level effects of losing species while adequately quantifying their effects on the ecosystem by experimental manipulations. Taylor et al. (2006) used in-stream experiments to show the consequences of losing a key fish consumer that is heavily harvested on whole-river carbon dynamics of in Venezuelan rivers. With this manipulation they were able to demonstrate that overharvesting the fish to the point of extirpation would result in significantly altered carbon dynamics at the reach-scale.

Ecosystem-level effects of species loss or decline can be scale-dependent. If the species in question has a wide range (e.g., migratory) consequences can be significant at the landscape scale. A common example are anadromous salmonids in the Western region of United States. Habitat fragmentation has led to strong population declines, with broad ecosystem-level effects across the landscape (Gresh et al. 2000, Zeug et al. 2011). One of the main consequences of salmon extirpations and declines is the reduction of marine-derived nutrient inputs into the watershed. These nutrients are essential to ecosystem function (e.g. primary production, nutrient cycling) in headwater streams (where salmon spawn) as well as adjacent riparian zones (Wold and Hershey 1999, Helfield and Naiman 2001, Naiman et al. 2002, Mitchell and Lamberti 2005, Kohler et al. 2008). In Central America, amphibian populations have been declining over the last decades due to a fungal disease (Whiles et al. 2013). These amphibian declines are known to have severe consequences at the ecosystem level in high elevation streams where tadpoles, one of the most important consumers in the system, are linked to various ecosystem properties and processes such as algal standing stocks, respiration rates, and nutrient cycling (Connelly et al. 2008, Whiles et al. 2013).

Dams are a major anthropogenic stressor to freshwater system that directly relate to species loss (e.g. Pringle et al. 2000). From changes in the hydrologic regime and the homogenization of river habitats (Poff et al. 2007) to the facilitation of the introduction and establishment of invasive species (Johnson et al. 2008), dams are widely recognized as a direct threat to biological diversity when not properly managed. Migratory species are particularly vulnerable due to blocking by dams that restrict their movement and dispersal through the landscape (Holmquist et al. 1998).

On the island of Puerto Rico, where streams are dominated by migratory shrimps and fishes, many of the river networks contain large dams constructed decades ago (Greathouse et al. 2006a). While these dams block the access of native migratory biota to headwater streams, there are still major rivers on the island that remain unaltered. This creates the ideal scenario to quantify effects of long-term species loss on stream ecosystem processes, while still having appropriate free-flowing reference streams where the system is relatively undisturbed.

In this study we examine the consequences of large dams on the key ecosystem process of decomposition across the island of Puerto Rico., Previous studies have shown that leaf decomposition rates in relatively free-flowing (lacking large dams) headwater streams are enhanced by native migratory shrimp macroconsumers (March et al 2000, Crowl et al 2001).We address the questions: (1) Are rates of leaf decomposition negatively affected by the decades-long extirpation of freshwater shrimp assemblages above large dams at landscape scales in Puerto Rico's central mountain range?; and (2) have other stream organisms provided functional redundancy by compensating for the loss of shrimps and similarly enhancing decomposition rates? To answer these questions, we combine two approaches: (1)*in situ* leaf decomposition experiments, in two focal streams (one dammed and one undammed), that manipulate the presence and absence of shrimp consumers; and (2) a landscape scale study of leaf decomposition rates in dammed (shrimp absence) and undammed (shrimp presence) streams across the island of Puerto Rico. We hypothesize that (1) leaf decomposition rates will be significantly higher in free-flowing undammed streams (relative to dammed streams) due to the presence of native shrimp assemblages which are key players in the decomposition process; and (2) other invertebrates, such as shredding aquatic insects, will **not** compensate for the loss of shrimps by providing functional redundancy and enhancing rates of leaf decomposition.

Methods

Study site

We examined tropical headwater streams located within the central mountain region, and the northeastern El Yunque National Forest reserve (hereafter EYNF) on the island of Puerto Rico (Figure 3.1). These high elevation forested regions receive a mean annual precipitation of 3500 mm with only a slight seasonal variation. Lowest annual rainfall typically occurs between January and April (Larsen 2000). River networks in Puerto Rico are typical of small Caribbean islands in that they are very steep and short compared to other tropical regions. This often results in a very distinct riffle and pools sequence. Benthic substrate is typically composed of bedrock and large boulders with pebble, sand, and silt in pool habitats. Canopy cover is very dense (>80%) and most of the energy is derived from allochthonous leaf material and woody debris falling into the stream. However, primary production can be a very important energy source for the food web even under these conditions (March and Pringle 2003).

The large-bodied native stream community is composed of ten species of fish and 17 species of decapods (Cooney and Kwak 2013, Perez-Reyes et al. 2013). Most of these organisms have an amphidromous life cycle, where the adults live in streams and rivers and release eggs and larvae that drift passively downstream to the ocean. Once in the marine environment, larval development occurs and juveniles eventually crawl and swim back into the stream network, traveling upstream (Chace and Hobbs 1969). All of the shrimp taxa in Puerto Rico are amphidromous, and genetic studies indicate that they do not necessarily return to their stream of origin, contrary to other commonly known anadromous species (Cook et al. 2009). This suggests that populations are mixed once the larvae reach the marine environment. The only two large stream organisms that are not amphidromous are the catadromous American eel (*Anguilla rostrata*), and the non-migratory freshwater crab (*Epilobocera sinuatifrons*).

Freshwater shrimps are the most common and abundant of all large stream organisms in Puerto Rico. The 17 different species fall within three families: Xiphocarididae (one species, *Xiphocaris elongata*), Atyidae (ten species), and Palaemonidae (six species). Most shrimp species are omnivorous with diets ranging from algae and detritus to smaller invertebrates (Covich and McDowell 1996). Feeding guilds and mechanisms differ widely among families. Atyidae are versatile in their feeding behavior and can be classified as filterers, collectors, and scrapers. They can switch between scraping benthic substrate with their chelae to filter-feeding by extending their chelae perpendicular to the water flow. In contrast, Xiphocaridae are classified as shredder/predators and Palaemonidae are considered collectors and predators. The latter mainly during their adult stages after developing a large pincer that they use to capture smaller prey.

Streams draining Puerto Rico have a high number of dams and water intakes that not only alter the natural flow regime but also represent a major barrier to the dispersal and recruitment of migratory organisms (Cooney and Kwak 2013, Benstead et al 1999).

Large dams (wall height >15m) with no spillway discharge are of particular concern (March et al. 2003) addd Greathouse 2006 since they total block migration of native migratory macrobiota . Puerto Rico has a high density of large dams mainly used for municipal water supply. As of 2006, Puerto Rico ranked at the top of all tropical countries in terms of density of large dams with a total of 26 for an average of 28.55 dams/ 10,000 km^2 (Greathouse et al. 2006a). Holmquist et al. (1998) surveyed native migratory shrimp populations across the island in 6 streams upstream from large dams and 6 streams without a downstream dam. They found that dams without a functional spillway discharge resulted in the complete loss of connectivity between headwater streams and the ocean leading to the extirpation of shrimps from these stream reaches. These extirpations result in severe consequences on ecosystem properties due to the absence of top-down control on basal resources by shrimps. Greathouse et al. (2006) showed that pools in streams above large dams have significantly higher benthic levels of algae, organic matter, inorganic matter, Carbon, and Nitrogen.

Experimental macroconsumer exclusion in focal streams

We ran 25-day *in situ* leaf decomposition experiments in each of two focal streams, one dammed (Quebrada Limón [18.15°N, 66.44°W]), and one undammed (Río Caín [18.12°N, 67.01°W])(Figure 3.1). Both streams are high-gradient second-order streams with similar chemical and physical characteristics (Table 3.1). We identified a 100 m reach in each stream and divided it into seven sections, each containing at least one pool with similar morphological characteristics. To exclude shrimp assemblages we used an *in situ* electric exclusion technique (Pringle et al. 1993, Greathouse et al. 2006b). Each pool contained an exclusion and a control frame modified from Marshall et al. (2012). Frames were made from uninsulated thick copper wire molded into a square ($0.1225\ m^2$) with a center ring (15cm diameter) held together with plastic zip ties and attached to the stream bed with rebar. Exclusion frames were attached to a 12 volt battery-operated electric fence charger (ParMak MAG.12-SP, Parker-McCrory USA) with insulated copper cables. Control frames were secured to the closest tree. After placing eight leaf packs of *Cecropia schreberiana* (average dry weight = 4.11 g; n=230) within each frame, we turned on the electricity of the exclusion frame. Each leaf pack was held together with a binder clip, thus avoiding the use of mesh netting to allow for full access of shrimps. Leaf packs were retrieved from each frame after 2, 5, 10, 14, 17, 20, 23, and 25 days of incubation in the stream. We collected leaf packs using a hand net (mesh size = 500 µm) to avoid losing any invertebrate that may have colonized the pack. Electricity was briefly turned off during leaf pack retrieval and it was noted that the presence of a person in the area was enough to prevent the shrimps from entering the frame. The electricity was turned back on as soon as leaf packs were collected. Each pack was placed inside a plastic bag, transported on ice, and processed in the laboratory within 24 hours. All insects found within each pack were identified to family and measured using a standard grid under 5x magnification. Biomass was estimated using published length-mass regressions (Benke et al. 1999). Leaf material from each pack was rinsed, dried for 24 hours at 65°C, and weighed. Finally, a subsample of the dried leaf material was weighed, burned at 500°C for 1 hour, and weighed again to estimate ash free dry mass (AFDM) remaining.

Landscape scale study of leaf decomposition across the island

To assess potential patterns in leaf decomposition rates across the island in both dammed and undammed streams, we ran 30-day leaf decomposition experiments in 14 study streams across the island, with seven dammed and seven undammed (Table 3.2). This includes the two focal streams in which the shrimp exclusion experiments were conducted.

We chose study stream reaches (Figure 1) that were located within ten major drainages across the island. Specific reaches were selected based on existing background information on faunal composition indicated by previous studies (Holmquist et al. 1998, Greathouse et al. 2006b); and physical and chemical characteristics within a given range (Table 3) All reaches were first-second order, high gradient, located above 300m.a.s.l., and with a mean temperature of x ± x (Tables 2,3). We selected a 50m reach in each study stream and identified four pools within each reach to set up replicate leaf pack clusters. Prior to the experiment we set up minnow traps in each pool (mesh size = 0.36 cm^2) to confirm the presence and absence of shrimps and estimate their abundance and biomass. Traps were deployed at a density of 0.5 traps per square meter, baited with dry cat food, and left overnight for shrimps to enter them (Cross et al. 2008a). All traps were retrieved the next morning, shrimps identified to genus, and carapace lengths measured prior to retuning individuals to the stream. We estimated shrimp biomass from length-mass regressions developed by March (2000). To estimate leaf decomposition rates we used the same methods from the previously described exclosure experiments, with two differences: (1) Leaf packs were attached to a string loop instead of a copper frame when attached to the stream bottom with rebar; and (2) we deployed five rather than eight leaf packs per pool and collected them after 3, 7, 13, 20, and 30 days. We also collected and processed all insects colonizing leaf packs using the same method as previous exclosure experiments.

Statistical analyses

Leaf breakdown rates for all experiments were calculated using the exponential decay model: $M_t = M_0\, e\text{-}^{kt}$, where M_t is the mass at time t and M_0 is the initial dry mass. The breakdown rate coefficients (expressed as k) was calculated as the slope of the line fitting the percent AFDM remaining (log-transformed) versus time (t) in days. We calculated one k for each frame in the reach-scale experiment (n=7 exclusion and n=7 control per stream), and for each pool in the landscape-scale (n=4 per stream). In the reach-scale exclusion experiment we analyzed each stream independently to evaluate the difference in decomposition rates between exclusion and control frames. Each pool was used as an independent unit and decomposition rates differences were analyzed with a single paired t-test for both streams. To directly compare the magnitude of the differences between dammed and undammed streams we used a two-way ANOVA classifying dam status (dammed or undammed) as the primary treatment. In the landscape scale study, we used each stream as a replicate unit. Leaf decomposition rates were analyzed using a t-test between dammed and undammed streams. Effects of shrimp abundance and biomass on leaf decomposition rates in undammed streams were analyzed using linear regressions. For both experiments, we analyzed differences in the abundance and biomass of insects colonizing the leaf packs between dammed and undammed streams using a Kruskal-Wallis test.

Results

Leaf decomposition exclosure experiments in focal streams

We found the three major families of shrimps within the undammed focal stream, while no shrimp occurred in the dammed focal stream (Table 3.1). *Xiphocaris elongata* was the most abundant taxon (9.17 ± 2.04 individuals m^{-2} , 4.63 ± 0.87 g m^{-2}), followed by Atyidae (4.67 ± 1.95 individuals m^{-2} , 3.88 ± 1.21 g m^{-2}), and Palaemonidae (1.73 ± 0.53 individuals m^{-2} , 1.20 ± 0.36 g m^{-2}). Observations of each electric exclusion frame during the experiment confirmed that shrimps were effectively excluded, while control (unelectrified) frames were constantly visited by shrimps. Each frame pair (one control and one electric exclusion) was observed for at least 5 minutes during each field visit (n=12) to confirm exclusion and visitation.

In the undammed focal stream, mean decomposition rate was significantly higher ($P <.0.001$) in the control ($k= 0.016 \pm 0.002$) versus the exclusion ($k= 0.012 \pm 0.001$) treatment . In contrast, there was no significant difference between the control ($k= 0.011 \pm 0.002$) and the exclusion ($k= 0.009 \pm 0.003$) treatment in the dammed focal stream. Overall, the highest mean decomposition rate occurred in the control treatment of the undammed stream ($F_{3,27} = 6.47$, $P < 0.001$; Figure 3.2).

A total of six different insect families were found within leaf packs in the undammed focal stream, and seven in the dammed focal stream for both treatments (exclusion and control). Our analysis considered those insect families that were found in at least six out of the eight sampling dates. The remaining taxa never occurred in samples on more than two sampling days and their mean abundance was always less than 1.5 individuals leaf pack^{-1}. In the undammed stream, the dominant families within both the exclusion and control treatments were: Leptophlebiidae (exclusion = 3.11 ± 0.47 individuals leaf pack^{-1}, 2.89 ± 0.77 mg AFDM leaf pack^{-1}; control = 2.93 ± 0.63 individuals leaf pack^{-1}, 2.63 ± 0.47 mg AFDM leaf pack^{-1}), Calamoceratidae (exclusion = 1.38 ± 0.61 individuals leaf pack^{-1}, 1.27 ± 0.31 mg AFDM leaf pack^{-1}; control = 0.94 ± 0.82 individuals leaf pack^{-1}, 0.88 ± 0.51 mg AFDM leaf pack^{-1}), and Chironomidae (exclusion = 0.59 ± 0.12 individuals leaf pack^{-1}, 0.64 ± 0.17 mg AFDM leaf pack^{-1}; control = 0.40 ± 0.31 individuals leaf pack^{-1}, 0.33 ± 0.15 mg AFDM leaf pack^{-1}). In the dammed stream, the dominant families within both the electric exclusion and control treatments were Chironomidae (exclusion = 2.49 ± 0.55 individuals leaf pack^{-1}, 2.11 ± 0.69 mg AFDM leaf pack^{-1}; control = 2.79 ± 0.73 individuals leaf pack^{-1}, 1.93 ± 0.39 mg AFDM leaf pack^{-1}), Calamoceratidae (exclusion = 1.17 ± 0.41 individuals leaf pack^{-1}, 0.74 ± 0.24 mg AFDM leaf pack^{-1}; control = 1.03 ± 0.34 individuals leaf pack^{-1}, 0.59 ± 0.20 mg AFDM leaf pack^{-1}), and Gyrinidae (exclusion = 1.39 ± 0.21 individuals leaf pack^{-1}, 1.08 ± 0.29 mg AFDM leaf pack^{-1}; control = 1.19 ± 0.37 individuals leaf pack^{-1}, 0.88 ± 0.47 mg AFDM leaf pack^{-1}). Neither abundance, nor biomass of individual families, and total insects colonizing leaf packs were significantly different between the treatments for neither stream ($p>0.05$; Figure 3.3).

Island-wide leaf decomposition rates

We found the three main families of shrimp in all of our seven undammed study streams, and none occurred in any of the seven dammed study streams. Mean abundance and biomass for all families had similar values to those of the focal streams used for experimental manipulations of shrimp presence and absence, with *Xiphocaris elongata* as the most abundant group (8.28 ± 2.55 individuals m^{-2} , 3.78 ± 1.05 g m^{-2}), followed by Atyidae (4.11 ± 2.22 individuals m^{-2} , 3.29 ± 1.71 g m^{-2}), and Palaemonidae (0.95 ± 0.81 individuals m^{-2} , 1.01 ± 0.70 g m^{-2}). Mean decomposition rate was significantly higher in the undammed ($k=0.0264$) versus dammed study streams($k= 0.0159$, $P< 0.001$; Figure 3.4). While some leaf packs were lost in three out of 14 study streams throughout the incubation period, we were still able to estimate decomposition rates in two of them where the experiment lasted 20 instead of 30 days (Table 3.4). One of the undammed study streams (Guayanilla) lost more than one complete day of sampling and since we were not able to collect leaf packs from this site after day 13, we consequently did not include it in mean estimates or statistical analyses. Leaf breakdown rates in undammed study streams were significantly related to shrimp abundance ($r^2 = 0.63$, $p< 0.001$; Figure 3.5 A) and biomass ($r^2 = 0.56$, $p < 0.001$; Figure 3.5 B).

Six different insect families colonized leaf packs across all seven undammed and five dammed study streams. Only three insect families (Leptophlebiidae, Chironomidae, and Calamoceratidae) were common in both dammed and undammed study streams. While mean total insect abundance was significantly higher in streams with a downstream dam ($P< 0.05$), the difference in mean biomass between the dammed and undammed streams was not significant ($P > 0.05$; Figure 3.6). Chironomidae abundance and biomass was significantly higher ($P < 0.05$) in streams with a downstream dam (Figure 3.6). There was no significant difference in abundance or biomass between dammed and undammed streams for Calamoceratidae. However, one of the dammed streams (Naranjo-B) had a particularly high abundance and biomass of the insect shredder (*Phylloicus pulchrus*) relative to the rest of the study streams (Figure 3.7).

Discussion

Our findings strongly suggest that shrimp extirpations upstream of dams have a significant negative effect on rates of leaf decomposition at the landscape scale across the island of Puerto Rico. There are a total of 26 large dams on the island and it is estimated that 27% of the total kilometers of drainage networks are located above them (Snyder et al. 2011;Figure 3.8). Most of the headwaters streams fall within that 27%, so the majority of low-order streams across the island are experiencing the effects of shrimp extirpations.

We found a significant indirect effect of dams on the ecosystem process of leaf decomposition. Large dams result in significant lower rates of leaf decomposition in upstream headwater reaches as a consequence of the extirpation of shrimp assemblages. As we predicted the experimental *in-situ* manipulations (macroconsumer exclusions) resulted in decreased leaf decomposition rates in the undammed stream where shrimp assemblages are abundant in contrast to the dammed stream where there was no difference in leaf decomposition rate between the exclusion and control treatment. Our landscape-scale prediction was also confirmed. Undammed streams had a significantly higher leaf decomposition rate and this pattern was constant across the island. Dammed streams showed much lower leaf decomposition rates and this pattern held true island-wide with the exception of one case that we discuss below. Our result not only linked the decreased leaf decomposition rates to the extirpation of shrimp assemblages by using *in situ* manipulations, but also showed that there are no other macroinvertebrates that could replace their role in the decomposition process. Our island-wide study also shows that this decrease in leaf breakdown rates is extended into the landscape scale to another streams where shrimps have been extirpated, and that the magnitude of this effect is constant throughout all these stream reaches.

The magnitude of the effects shrimp extirpations on leaf decomposition rates across the island are similar to those previously reported for Puerto Rican streams using small-scale manipulations in streams within EYNF where shrimps are found in stable populations in a prime and protected habitat (March et al. 2001). Excluding shrimps from small sections from streams in the EYNF resulted in a reduction of *Cecropia scheberiana* leaf decomposition rate of 38% compared to stream sections where shrimp had access. In our study, we used the same leaf species and the extirpation of shrimps from reaches above large dams resulted in a reduction of 41% compared to undammed streams. There is also previous evidence that this reduction in decomposition rates could be directly related to their abundance and biomass (Crowl et al. 2001b) just as our landscape scale data from undammed streams suggests. Further evidence provided by a laboratory experiment showed that shrimp contribution to the decomposition process will differ between the species within the assemblage (March et al. 2001). They showed that *Xiphocaris elongata* is the species that contributed the most to the leaf decomposition process compared to other shrimp species and all possible combinations within the assemblage. Although we were not able to isolate the taxa-specific contribution to leaf decomposition in any of our experiments, *Xiphocaris elongata* was the most abundant species in our shrimp surveys and their effects are not neglected when other shrimp species are present (March et al. 2001). Also, all native shrimps species in Puerto Rico share the amphidromous life history, so it is not essential to differentiate their effects of by taxa since all the species are being extirpated under the same conditions, and there is no evidence that a particular taxa would have an advantage.

The lower decomposition rates that we observed in streams above large dams may have significant indirect implications for carbon cycling. A reduced breakdown rate might also mean a longer storage period of coarse particulate organic matter (CPOM) and a reduced downstream transport of fine particulate organic matter (FPOM). Both of these issues could lead other ecosystem-level effects such as an increase in respiration rates due to the higher amount of slower decomposing detritus, and decline in nutrient demand resulting from the associated decrease in net primary production. For downstream reaches it can result in a reduced input of energy to assemblages depending from upstream sources by reducing the total input of drifting FPOM and the average particle size reaching those areas.

Our data suggest that a similarity in leaf breakdown rate between one of our dammed sites (k= 0.0235) to the average rate in undammed streams (k=0.0264) was due to a particularly high abundance of *Phylloicus pulchrus* larvae. *Phylloicus* can be important shredders in Puerto Rican streams (Rincon and Covich 2014) and Neotropical streams in general where it is widely recognized for its shredding feeding behavior and contribution to decomposition of course particulate organic material (Rincón and Martínez 2006, Encalada et al. 2010, Rincon and Covich 2014), Murray et al. 2018, Simon et al. 2019). However, the high abundance of this taxon in one of our study streams is not necessarily related to the absence of shrimps or the presence of a downstream dam. *Phylloicus* distribution is naturally very patchy and usually directly related to the availability of leaf litter in depositional areas of the stream and other studies from Puerto Rican streams have shown that they can be present even under high shrimp densities (Ramirez and Hernandez-Cruz 2004).

Although *Phylloicus* may have directly influenced the high decomposition rates for that single site above dam, it shouldn’t be considered as a case for potential functional redundancy to the extirpated shrimp assemblage. Greathouse et al. (2006) found a change to the overall insect structure and higher biomass levels in headwater streams located above large dams in Puerto Rico. However, these changes were described from samples including all habitats and substrates available in the system and we did not find any of these difference in our insect samples collected from leaf packs. The changes in insect assemblage are most likely associated to the changes in benthic resources (i.e. higher FPOM, CBOM, and epilithic algae) from hard substrate as a result of losing shrimp top-down control but are not reflected in leaf litter and other CPOM substrates. Thus, it is unlikely for *Phylloicus* to take over the decomposition role of the shrimps even after decades of the dams being in place.

Leaf decomposition in tropical streams is strongly linked to shredders presence (Rincon and Covich 2014) the fact that no shredders are replacing the shrimp’s niches in the system results in significantly lower decomposition rates. There was no significant difference in shredder abundance in our leaf packs between the dammed and undammed streams. Greathouse et al (2006) also found no difference between dammed and undammed stream reaches in their study. Besides the insect assemblages, there are no other assemblages in Puerto Rican streams above dams that may be able to make up for the extirpation of shrimps. A possible macroconsumer that can influence decomposition in streams above large dams may be introduced fish species. For example, the redbreast tilapia (*Tilapia rendalli*) are generalists who may feed on vegetative detritus and are common in streams above large dams (Cooney and Kwak 2013). However, we focused in high-elevation high-gradient sites where shrimps are more abundant and their effect is more noticeable (Greathouse et al. 2006, March et al. 2001) and besides the native gobies, other fish do not reach these stream reach locations. Native fishes are also not an option since most species are also amphidromous and are also extirpated from these reaches.

The most logical candidate would be the native freshwater crab (*Epilobocera sinuatifrons*), as these are the only non-migratory native macroconsumer and their population distribution is not significantly affected by the presence of a downstream dams. These freshwater crabs are also considered omnivorous and are known to feed on detritus material (Covich and McDowell 1996) however, there is no evidence that they consume it in large amounts to do a significant impact on the whole system. Also, their relative abundance is significantly lower compared to all species within the shrimp assemblage (Perez-Reyes et al. 2013).

Dams cause dramatic changes to the physical environment of the streams and rivers and these effects could be extended across the whole hydrologic network (Poff and Hart 2002). These changes in abiotic factor could cause significant ecosystem-level changes either similar or completely different that the indirect effects of shrimp extirpations. Changes in habitat complexity, as in the change from a lotic to a lentic system, often result in changes to community composition and hence changes in ecosystem properties. In our study we tried to eliminate any possible confounding factor associated to these changes in the physical environment by using only high gradient headwater streams located high in the watershed. Previous studies looking at the effects of shrimp assemblages on ecosystem properties and processes along an altitudinal gradient showed that strong effects by the shrimps are more prevalent in high elevation streams. This pattern has been shown for leaf decomposition (March et al. 2001), top-down control of benthic resources (March et al. 2002), and food web structure (March and Pringle 2003). This differences in the effect magnitude is caused by the significantly higher abundance and biomass of shrimp assemblages in these upper stream reaches compared to low elevation streams. This specific distribution is related to the availability of spatial refugia from stream predators that are not able to reach high gradient streams (Covich et al. 2009). Thus, if abiotic changes by dams would cause significant effect on ecosystem-level parameters this would not affect our results since most of these would be reflected in low gradient streams closer to the reservoir. This was confirmed by Greathouse et al. (2006c) when they measure basal resources in low-gradient streams in dammed and undammed streams and found that there was not a significant difference in mean concentration levels between the two types of streams as they found in their high-gradient high elevation sites.

There are still major river networks in Puerto Rico that to this date don't have any large dams or other structure blocking the migration of amphidromous fauna. These networks maintain viable populations of shrimps and do not experience the negative changes in ecosystem structure, properties, or processes. Since it is known that shrimps are not site faithful (Cook et al. 2009), these undamaged networks could serve as source for rivers that are currently blocked by dams. There are ways to mitigate and resolve the extirpation of shrimps by dams with the proper management practices without compromising the social purpose of the structure itself (Benstead et al. 1999, March et al. 2003). Previous studies showed that, in Puerto Rico, large dams cause a significant change in the community structure by extirpating native macrobiota from upstream reaches (Holmquist et al. 1998) and this resulted in an indirect negative effect on ecosystem-level properties as measured by the significantly higher levels of algae, benthic organic matter and sediment (Greathouse et al. 2006c). This is the first study to show a significant effect on ecosystem processes linked to shrimp extirpations at the landscape-scale.

References

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-Mass Relationships for Freshwater Macroinvertebrates in North America with

Particular Reference to the Southeastern United States. Page 308. North American Benthological Society.

Benstead, J. P., W. F. Cross, J. G. March, W. H. McDowell, A. Ramirez, and A. P. Covich. 2010. Biotic and abiotic controls on the ecosystem significance of consumer excretion in two contrasting tropical streams. Freshwater Biology 55:2047-2061.

Benstead, J. P., J. G. March, C. M. Pringle, and F. N. Scatena. 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. Ecological Applications 9:656-668.

Chace, F. A., and H. H. Hobbs. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica [by] Fenner A. Chace, Jr., and Horton H. Hobbs, Jr. Washington, D.C. : Smithsonian Institution Press.

Connelly, S., C. M. Pringle, R. J. Bixby, R. Brenes, M. R. Whiles, K. R. Lips, S. Kilham, and A. D. Huryn. 2008. Changes in Stream Primary Producer Communities Resulting from Large-Scale Catastrophic Amphibian Declines: Can Small-Scale Experiments Predict Effects of Tadpole Loss? Ecosystems 11:1262-1276.

Cook, B. D., S. Bernays, C. M. Pringle, and J. M. Hughes. 2009. Marine dispersal determines the genetic population structure of migratory stream fauna of Puerto Rico: evidence for island-scale population recovery processes. Page 709.

Cooney, P. B., and T. J. Kwak. 2013. Spatial Extent and Dynamics of Dam Impacts on Tropical Island Freshwater Fish Assemblages. BioScience 63:176-190.

Covich, A., and W. H. McDowell. 1996. The Stream Community. Pages 434-459 *in* R. B. Waide and W. B. Reagan, editors. The food web of a tropical rainforest. University of Chicago Press, Chicago.

Covich, A. P., M. C. Austen, F. Barlocher, E. Chauvet, B. J. Cardinale, C. L. Biles, P. Inchausti, O. Dangles, M. Solan, M. O. Gessner, B. Statzner, and B. Moss. 2004. The role of Biodiversity in the functioning of freshwater and marine benthic ecosystems. BioScience 54:767-775.

Covich, A. P., T. A. Crowl, C. L. Hein, M. J. Townsend, and W. H. McDowell. 2009. Predator–prey interactions in river networks: comparing shrimp spatial refugia in two drainage basins. Freshwater Biology 54:450-465.

Creed, R. P., R. P. Cherry, J. R. Pflaum, and C. J. Wood. 2009. Dominant species can produce a negative relationship between species diversity and ecosystem function. Oikos 118:723-732.

Cross, W. F., A. P. Covich, T. A. Crowl, J. P. Benstead, and A. Ramirez. 2008a. Secondary production, longevity and resource consumption rates of freshwater shrimps in two tropical streams with contrasting geomorphology and food web structure. Freshwater Biology 53:2504-2519.

Cross, W. F., A. Ramírez, A. Santana, and L. Silvestrini Santiago. 2008b. Toward Quantifying the Relative Importance of Invertebrate Consumption and Bioturbation in Puerto Rican Streams. Biotropica 40:477-484.

Crowl, T. A., W. H. McDowell, A. P. Covich, and S. L. Johnson. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82:775-783.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews Of The Cambridge Philosophical Society 81:163-182.

Encalada, A. C., J. Calles, V. Ferreira, C. M. Canhoto, and M. A. S. Graca. 2010. Riparian land use and the relationship between the benthos and litter decomposition in tropical montane streams. Freshwater Biology 55:1719-1733.

Greathouse, E. A., C. M. Pringle, and J. G. Holmquist. 2006a. Conservation and management of migratory fauna: dams in tropical streams of Puerto Rico. Aquatic Conservation 16:695-712.

Greathouse, E. A., C. M. Pringle, and W. H. McDowell. 2006b. Do small-scale exclosure/enclosure experiments predict the effects of large-scale extirpation of freshwater migratory fauna? Oecologia 149:709-717.

Greathouse, E. A., C. M. Pringle, W. H. McDowell, and J. G. Holmquist. 2006c. Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico. Ecol Appl 16:339-352.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An Estimation of Historic and Current Levels of Salmon Production in the Northeast Pacific Ecosystem: Evidence of a Nutrient Deficit in the Freshwater Systems of the Pacific Northwest. Fisheries 25:15-21.

Helfield, J. M., and R. J. Naiman. 2001. Effects of Salmon-Derived Nitrogen on Riparian Forest Growth and Implications for Stream Productivity. Ecology:2403-2409.

Holmquist, J. G., J. M. Schmidt-Gengenbach, and B. B. Yoshioka. 1998. High dams and marine-freshwater linkages: Effects on native and introduced fauna in the Caribbean. Conservation Biology 12:621-630.

Johnson, P. T. J., J. D. Olden, and M. J. vander Zanden. 2008. Dam invaders: impoundments facilitate biological invasions into freshwaters. Frontiers in Ecology and the Environment 6:359-365.

Kohler, A. E., A. Rugenski, and D. Taki. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho, U.S.A. streams. Freshwater Biology 53:446-460.

Larsen, M. C. 2000. Analysis of 20th century rainfall and streamflow to characterize drought and water resources in Puerto Rico. Physical Geography 21:494-521.

March, J. G. 2000. The role of freshwater shrimps : patterns and processes along a tropical island stream continuum, Puerto Rico University of Georgia, Athens, GA.

March, J. G., J. P. Benstead, C. M. Pringle, and M. W. Ruebel. 2001. Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. Canadian Journal of Fisheries & Aquatic Sciences 58:470.

March, J. G., J. P. Benstead, C. M. Pringle, and F. N. Scatena. 2003. Damming Tropical Island Streams: Problems, Solutions, and Alternatives. BioScience 53:1069-1078.

March, J. G., and C. M. Pringle. 2003. Food web structure and basal resource utilization along a tropical island stream continuum, Puerto Rico. Biotropica 35:84-93.

March, J. G., C. M. Pringle, M. J. Townsend, and A. I. Wilson. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. Freshwater Biology 47:377-390.

Marshall, M. C., A. J. Binderup, E. Zandona, S. Goutte, R. D. Bassar, R. W. El-Sabaawi, S. A. Thomas, A. S. Flecker, S. S. Kilham, D. N. Reznick, and C. M. Pringle. 2012. Effects of consumer interactions on benthic resources and ecosystem processes in a neotropical stream. Plos One 7:e45230.

Master, L. L., B. A. Stein, L. S. Kunter, and G. A. Hammerson. 2000. Vanishing assets: conservation status of U.S. species. Pages 93-118 *in* B. A. Stein, L. S. Kunter, and J. S. Adams, editors. Precious heritage: the status of biodiversity in the United States. Oxford University Press, New York.

Mitchell, N. L., and G. A. Lamberti. 2005. Responses in Dissolved Nutrients and Epilithon Abundance to Spawning Salmon in Southeast Alaska Streams. Limnology and Oceanography 50:217-227.

Murray, K.M., D. Stoker, C. M. Pringle and T. N. Simon. 2018. Is spatial variation in population size structure of a stream-dwelling caddisfly due to the altered effects of a predator by a third-party species? Hydrobiologia. 820 (1): 65

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific Salmon, Nutrients, and the Dynamics of Freshwater and Riparian Ecosystems. 5:399-417.

Perez-Reyes, O., T. A. Crowl, P. J. Hernandez-Garcia, R. Ledesma-Fuste, F. A. Villar-Fornes, and A. P. Covich. 2013. Freshwater decapods of Puerto Rico: a checklist and reports of new localities. Zootaxa 3717:329-344.

Poff, N. L., and D. D. Hart. 2002. How Dams Vary and Why It Matters for the Emerging Science of Dam Removal. BioScience 52:659.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proc Natl Acad Sci U S A 104:5732-5737.

Pringle, C. M. 1996. Atyid shrimps (Decapoda: Atyidae) influence the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. Freshwater Biology 35:125.

Pringle, C. M., G. A. Blake, A. P. Covich, K. M. Buzby, and A. Finley. 1993. Effects of Omnivorous Shrimp in a Montane Tropical Stream - Sediment Removal, Disturbance of Sessile Invertebrates and Enhancement of Understory Algal Biomass. Oecologia 93:1-11.

Pringle, C. M., and T. Hamazaki. 1998. The role of omnivory in structuring a neotropical stream: Separating diurnal versus nocturnal effects. Ecology 79: 269-280.

Pringle, C. M., N. Hemphill, W. H. McDowell, A. Bednarek, and J. G. March. 1999. Linking species and ecosystems: Different biotic assemblages cause interstream differences in organic matter. Ecology 80:1860-1872.

Pringle, C. M., M. Freeman, and B. Freeman. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical-temperate comparisons BioScience 50: 807-823.

Ramirez, A., and L. R. Hernandez-Cruz. 2004. Aquatic insect assemblages in shrimp-dominated tropical streams, Puerto Rico. Biotropica 36:259-266.

Rincon, J., and A. Covich. 2014. Effects of insect and decapod exclusion and leaf litter species identity on breakdown rates in a tropical headwater stream. Rev Biol Trop 62 Suppl 2:143-154.

Rincón, J., and I. Martínez. 2006. Food Quality and Feeding Preferences of Phylloicus sp. (Trichoptera:Calamoceratidae). Page 209. North American Benthological Society.

Simon, T.N., R.D. Bassar, A. J. Binderup, A.S. Flecker, M. A. Marshal, S. A. Thomas, J. Travis, D.N. Reznick and C. M. Pringle. 2019. Landscape-scale patterns in top-down control of decomposition: Omnivory disrupts a tropical detrital-based trophic cascade. Ecology.

Smith, G. C., A. P. Covich, and A. M. D. Brasher. 2003. An Ecological Perspective on the Biodiversity of Tropical Island Streams. Pages 1048-1051 BioScience.

Snyder, M. N., E. P. Anderson, and C. M. Pringle. 2011. A migratory shrimp's perspective on habitat fragmentation in the neotropics: extending our knowledge from Puerto Rico. Pages 169-182 *in* A. Asakura, editor. New Frontiers in Crustacean Biology: Proceedings of the TCS Summer Meeting, Tokyo, 20-24 September 2009. Koninklijke Brill NV, The Netherlands.

Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of Freshwater Ecosystems by Bivalves. BioScience 49:19.

Strayer, D. L., and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society 29:344-358.

Taylor, B. W., A. S. Flecker, and R. O. Hall, Jr. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science 313:833-836.

Vaughn, C. C. 2010. Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging Conclusions and Research Directions. BioScience 60:25-35.

Whiles, M. R., R. O. Hall, W. K. Dodds, P. Verburg, A. D. Huryn, C. M. Pringle, K. R. Lips, S. S. Kilham, C. Colon-Gaud, A. T. Rugenski, S. Peterson, and S. Connelly. 2013. Disease-Driven Amphibian Declines Alter Ecosystem Processes in a Tropical Stream. Ecosystems 16:146-157.

Wold, A. K. F., and A. E. Hershey. 1999. Effects of salmon carcass decomposition on biofilm growth and wood decomposition. Canadian Journal of Fisheries and Aquatic Sciences 56:767-773.

Wright, M. S., and A. P. Covich. 2005. The Effect of Macroinvertebrate Exclusion on Leaf Breakdown Rates in a Tropical Headwater Stream. Biotropica 37:403-408.

Zeug, S. C., L. K. Albertson, H. Lenihan, J. Hardy, and B. Cardinale. 2011. Predictors of Chinook salmon extirpation in California's Central Valley. Fisheries Management and Ecology 18:61-71.

Tables

Table 3.1. Shrimp abundance and major physicochemical parameters at the two focal stream reaches during the reach-scale *in-situ* exclosures experiments. All values are mean (n=7 pools at each site) ± 1SE.

	Undammed (Río Caín)		Dammed (Quebrada Limón)	
Shrimp taxa (individuals m^{-2})				
Xiphocaris elongata	9.17	± 2.04	0	
Atya spp.	4.63	± 0.87	0	
Macrobrachium spp.	1.73	± 0.53	0	
Physical Parameters				
Discharge (L s^{-1})	15		17	
Width (m)	3.18	± 0.13	2.72	± 0.43
Depth (m)	0.54	± 0.15	0.46	± 0.08
Chemical Parameters				
Conductivity (us cm^{-1})	175		179	
NO_3 (µgN L^{-1})	376		471	
NH_4 (µgN L^{-1})	14.2		19.4	
SRP (µgP L^{-1})	19		16	

Table 3.2. List and general information of study sites used in the landscape-scale leaf decomposition experiment. There were no large dams downstream of our Undammed sites (NA = not applicable).

Study Sites	Main Watershed	Stream Order	Elevation (m)	Downstream Dam	Dam construction year	Km above dam
Undammed						
(1) Caín	Guanajibo	2	323	NA	NA	NA
(2) Guayanilla	Guayanilla	1	450	NA	NA	NA
(3) Orocovis	Grande de Manatí	1	806	NA	NA	NA
(4) Peñuelas	Tallaboa	2	375	NA	NA	NA
(5) Ponce	Inabón	2	504	NA	NA	NA
(6) Prieta	Espíritu Santo	2	560	NA	NA	NA
(7) Toro Negro		2	884	NA	NA	NA
Dammed						
(8) Carite	La Plata	1	690	Carite	1913	5
(9) Jayuya	Grande de Arecibo	2	877	Caonillas	1948	25
(10) Limón	Jacagüas	2	487	Toa Vaca	1972	10
(11) Matrullas	Grande de Manatí	1	809	Matrullas	1934	4
(12) Naranjo-A	Yauco	2	344	Luchetti	1952	4
(13) Naranjo-B	Yauco	1	383	Luchetti	1952	5
(14) Turabo	Grande de Loíza	2	310	Carraízo	1954	27

Table 3.3. Shrimp abundance and major physicochemical parameters at the 14 stream reaches during the landscape-scale leaf decomposition experiments. All values are mean (n=7 streams per category) ± 1SE.

	Undammed (n=7 streams)		Dammed (n=7 streams)	
Shrimp taxa (individuals m^{-2})				
Xiphocaris elongata	8.28	± 2.55	0	
Atya spp.	4.11	± 2.22	0	
Macrobrachium spp.	0.95	± 0.81	0	
Physical Parameters				
Discharge (L s^{-1})	17	± 1.34	13	± 1.96
Width (m)	2.38	± 0.13	2.03	± 0.43
Depth (m)	0.44	± 0.05	0.41	± 0.1
Chemical Parameters				
Conductivity (us cm^{-1})	215	± 33	179	± 89
NO_3 (μgN L^{-1})	428	± 112	492	± 97
NH_4 (μgN L^{-1})	17.2	± 1.03	11.4	± 2.87
SRP (μgP L^{-1})	19	± 2.77	27	± 6.90

Table 3.4. Leaf decomposition rate model coefficients for all the streams without a dam (n=7) and the streams located above a large dam (n=7) in the landscape-scale leaf decomposition experiment.

Site	Experiment length(days)	n (number of sampling dates)	Decomposition rate (k)	R^2	P-value
Undammed					
Caín	30	5	-0.0297	0.92	0.0098
Guayanilla*	13	3	-0.0302	0.94	0.1518
Orocovis	30	5	-0.0265	0.91	0.0129
Peñuelas	20	4	-0.0313	0.99	0.0049
Ponce	30	5	-0.0196	0.89	0.0169
Prieta	30	5	-0.0293	0.90	0.0129
Toro Negro	30	5	-0.0225	0.82	0.0337
Dammed					
Carite	30	5	-0.0149	0.85	0.0246
Jayuya	30	5	-0.0091	0.97	0.0023
Limon	30	5	-0.0088	0.95	0.0045
Matrullas	30	5	-0.0193	0.99	0.0004
Naranjo-A	20	4	-0.0235	0.90	0.0521
Naranjo-B	30	5	-0.0176	0.93	0.0088
Turabo	30	5	-0.0181	0.96	0.0037

** Data from only 3 of the 5 expected sampling dates due leaf packs lost.*

Figures

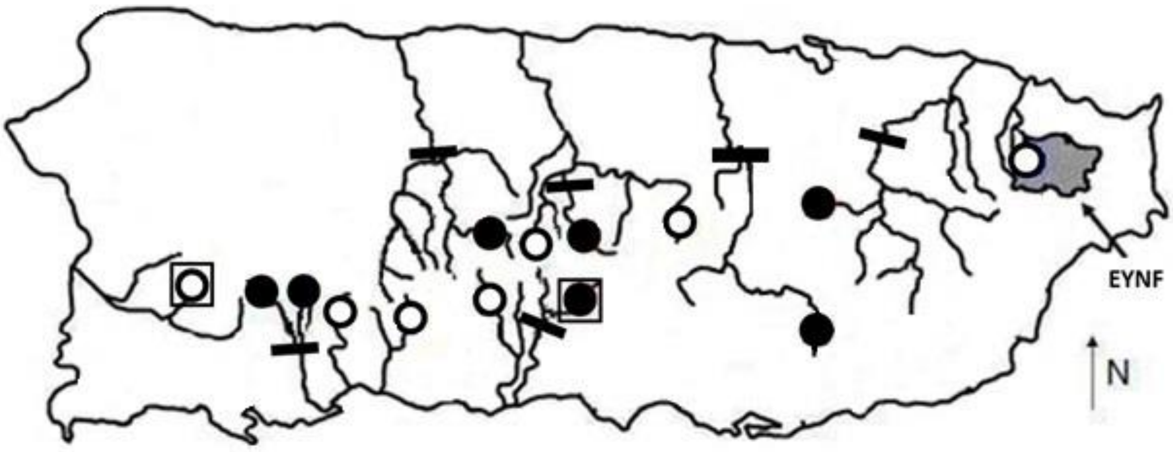

Figure 3.1. Map of Puerto Rico showing the location of the two focal streams used for the *in-situ* exclosures experiments, and the locations of the 14 study streams used for the leaf decomposition experiment at the landscape-scale above large dams. We used a total of 7 undammed streams (open circles) and 7 dammed streams (solid circles). The two focal streams used for the *in-situ* are enclosed by a square. Black rectangles are the location of the dams below our dammed study reaches. The gray shaded area in the Northeast is El Yunque National Forest (EYNF).

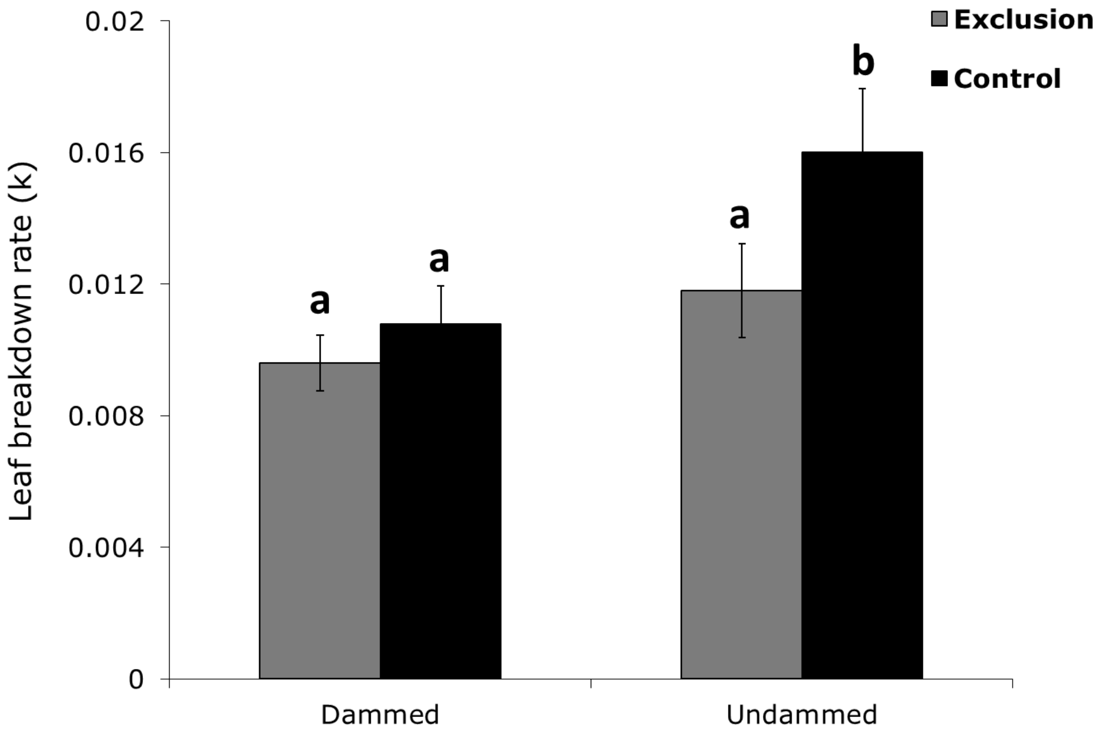

Figure 3.2. Mean (± 1SE) decomposition rates during the reach-scale *in situ* exclosures experiments. The gray bars (exclusion) are from the electrified frames treatments and the black bars (control) represent the open (non-electric) treatments where macroconsumers had access to our leaf packs. Difference in lowercases determine significant differences between the treatments ($P < 0.05$).

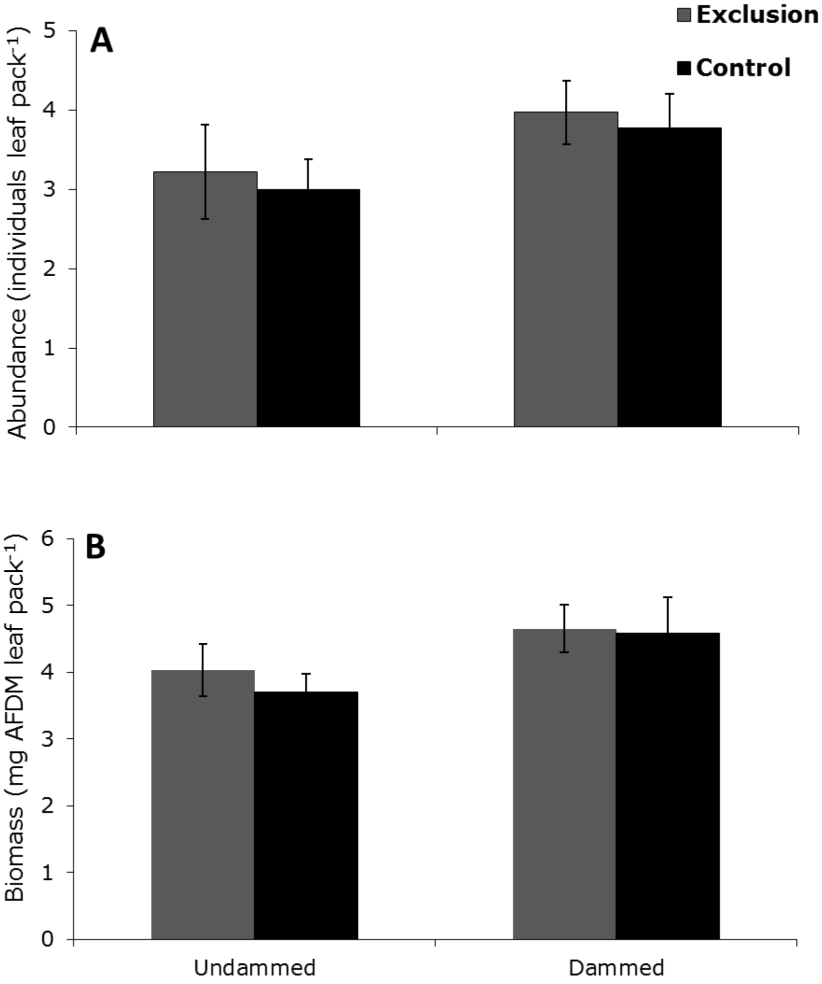

Figure 3.3. Mean (± 1SE) insect abundance (A), and biomass (B) found in leaf packs during the *in-situ* exclusion experiment in both (dammed and undammed) focal streams. The gray bars (exclusion) are from the electrified frames treatments and the black bars (control) represent the open (non-electric) treatments where macroconsumers had access to our leaf packs. Means were calculated from all the leaf packs collected for each treatment (n=56) throught the whole experiment (25 days).

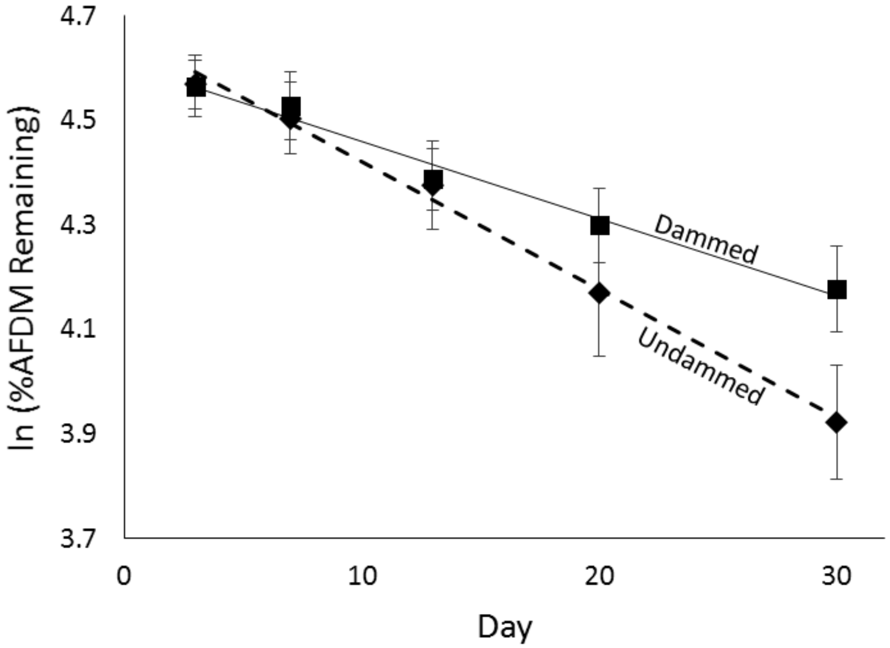

Figure 3.4. Combined mean (± 1SE) ln % AFDM remaining over time in leaf packs for all dammed (squares, solid line; n=7), and undammed streams (diamonds, dashed line; n=7) in the landscape-scale leaf decomposition study.

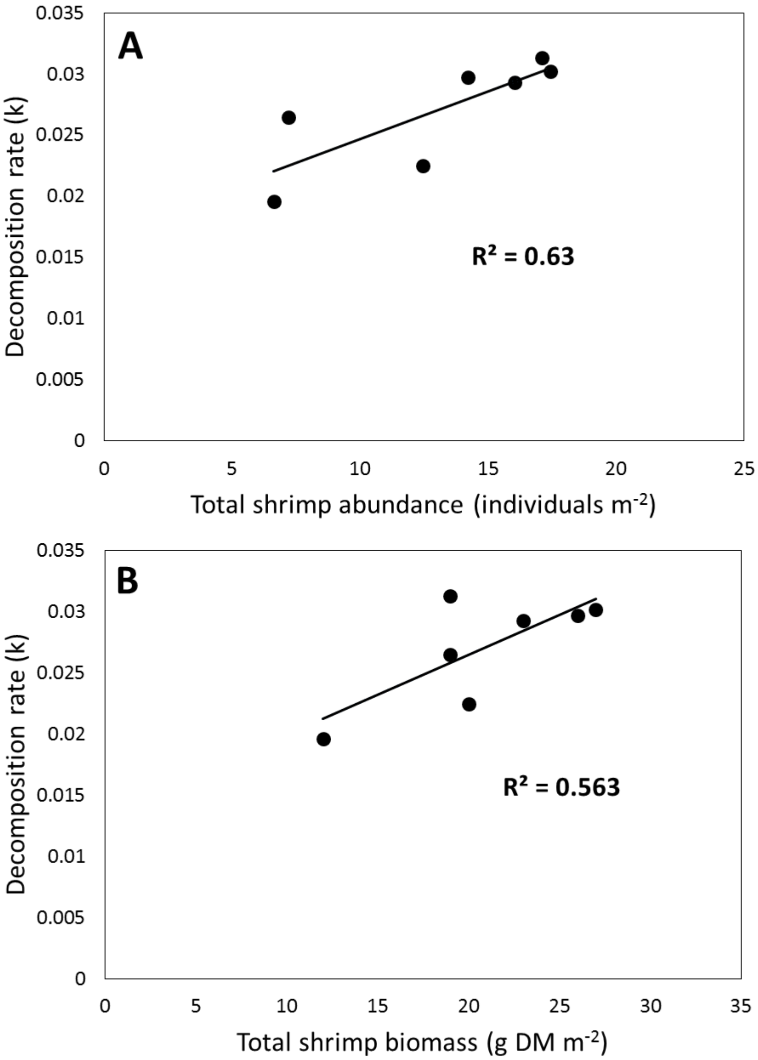

Figure 3.5. Linear regressions of shrimp density (A), and biomass (B) against leaf decomposition rate for all the undammed streams (n=7) in the landscape-scale leaf decomposition experiment.

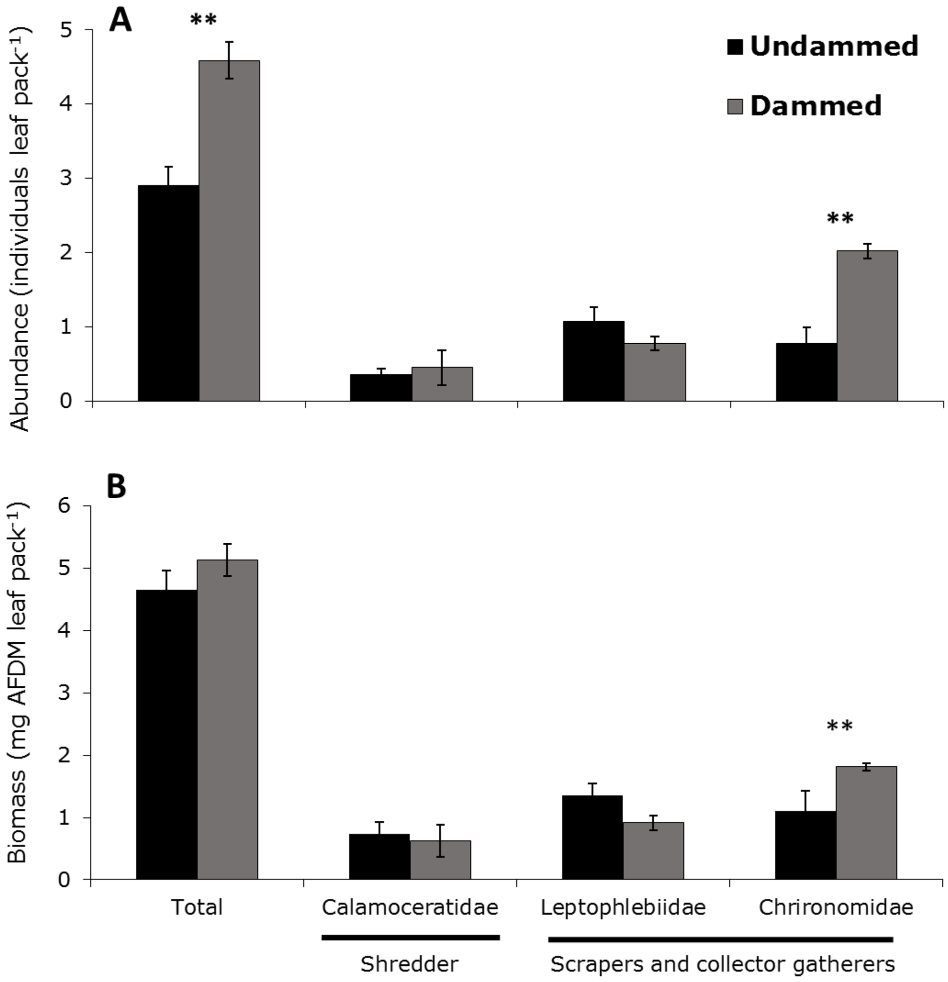

Figure 3.6. Means (± 1SE) total insect abundance (A), and biomass (B) found in leaf packs for both dammed (n=7) and undammed (n=7) streams during the landscape scale experiments. The three families included are the only ones found in both dammed and undammed streams. Means were calculated from all the leaf packs collected for each treatment throught the whole experiment (30 days). Significant differences ($P < 0.05$) between streams with dams and streams without dams are denoted by **.

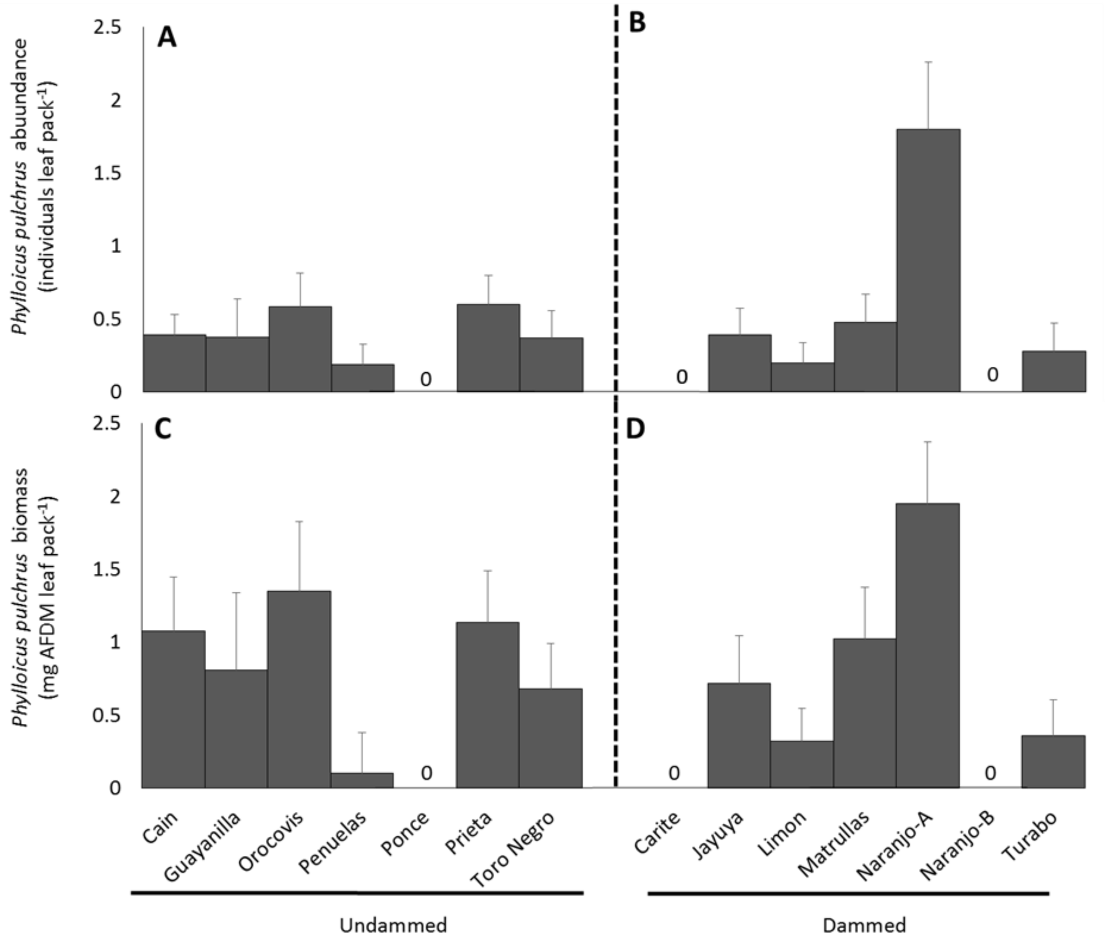

Figure 3.7. Mean (± 1SE) abundace (A & B) and biomass (C & D) of *Phylloicus pulchrus* (Trichoptera: Calamoceratidae) found in leaf packs during the landscape scale experiments for both dammed and undammed streams during the landscape-scale leaf decomposition experiments

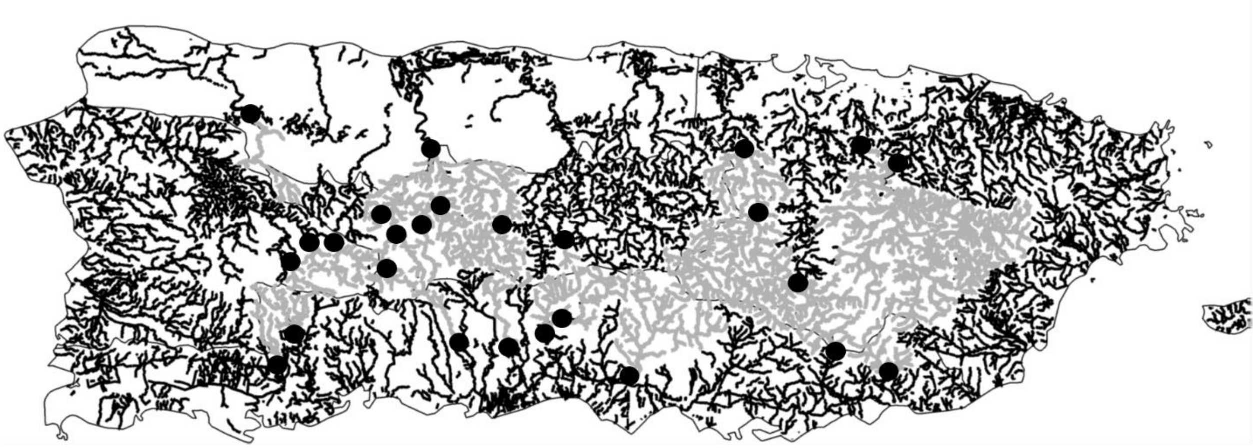

Figure 3.8. Map of the all the drainage networks and the location of all large dams (black circles) in Puerto Rico. Light shaded areas are all the stream reaches located above a large dam. This area totals 23% of all the drainage. Map modified from from Snyder et al. (2011)

CHAPTER 4

EXTIRPATION OF NATIVE STREAM MACROCONSUMERS EFFECTS ON REACH-SCALE NUTRIENT DYNAMICS IN TROPICAL HEADWATER STREAMS OF PUERTO RICO

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[1] Torres P.J. and C.M. Pringle. To be submitted to *Freshwater Science*

Abstract

In Puerto Rico, large dams are known to drastically change stream ecosystem structure and function. The lack of a spillway discharge or a fish passage on most dammed rivers create an impermeable barrier to the migration of amphidromous native consumers, eventually leading to their complete extirpation from upstream reaches. The most dominant migratory consumer group in Puerto Rican streams, and thus the most directly affected by this issue, are the native freshwater shrimps. We studied the effect of large-scale shrimp extirpations on Nitrogen and Phosphorus uptake rates in 6 different stream reaches (3 dammed and 3 undammed) by conducting short-term nutrient additions during the dry and wet seasons. Then, we used published values of species-specific nutrient excretion rates to estimate the direct contribution of shrimps to nutrient cycling and how this is lost in streams where they have been extirpated. We also selected a sub-set of streams (one dammed and one undammed) and ran whole-reach stream metabolism measurements. Streams above large dams showed longer nutrient uptake lengths for both Nitrogen and Phosphorus during the dry season while there were no significant differences during the wet season. Shrimp-specific contributions to whole-reach nutrient cycling were higher during the dry season mostly because their densities did not fluctuate between seasons. Whole-reach respiration was higher in streams above dams while net primary productivity was higher in undammed streams. Our results suggest that shrimps are affecting nutrient and metabolism dynamics both directly, by reducing the benthic algal and fine organic matter levels, and indirectly by partaking in the whole nutrient cycling dynamics through excretion. Also, our reach-scale findings could be an indication

that large-scale extirpations of the shrimp consumers are resulting in a landscape-level changes of the whole nutrient and metabolism dynamics around the whole island

Introduction

The importance of animals in ecosystem-level nutrient processes has been well established for freshwater systems (Vanni 2002, Capps et al. 2015). In streams, large bodied consumers can influence the movement of nutrients both directly through excretion (Hood et al. 2005, Small et al. 2011), and indirectly through consumption and bioturbation (Pringle and Hamazaki 1998, Crowl et al. 2001b, Simon et al. 2004). However, abiotic factors (e.g., discharge) also influence the cycling of nutrients, and in some cases they override the relative importance of consumers in this process (Benstead et al. 2010, Griffiths and Hill 2014). It is important to understand how biotic and abiotic controls interact and change over time since other ecosystem processes (e.g. primary production) are directly influenced by the availability and movement of nutrients, particularly nitrogen (N) and phosphorus (P). A change in any of the factors regulating nutrient processing in streams can indirectly affect other ecosystem processes at multiple scales (Taylor et al. 2012). Some common factors that can affect nutrient cycling processes in streams are the loss of species (McIntyre et al. 2007), direct anthropogenic alterations of the physicochemical environment (Kaye et al. 2006, Bukaveckas 2007, Mulholland et al. 2008), and alterations to the flow regime (Pinay et al. 2002). All of these can occur at random and the magnitude of the effect could range from local and short term, to landscape-scale and permanent. Thus, it is essential to incorporate time and seasonal variation when assessing these issues.

Consumers can regulate nutrient processes in streams both directly and indirectly, and the magnitude at which they do varies between species and systems. In terms of direct contribution, rates of nutrient excretion by consumers are normally influenced by the stoichiometric composition of their body and their food resources (Vanni et al. 2002, McManamay et al. 2011). Organisms with a high nutrient demand normally excrete nutrients at a lower rate. For example, vertebrates normally have relatively low P excretion rates compared to invertebrates due to higher P demand to support bone structure (Vanni 2002). In some cases, a single species or taxonomic group can regulate almost the entire dissolve nutrient flux in a system by acting as sinks (Capps and Flecker 2013) or by having a significantly high excretion rate (Small et al. 2011). Species with significant contribution to the dissolved nutrient pool through excretion usually have a very high individual mass-specific excretion rate and (Small et al. 2011). However, species or assemblages with low individual mass-specific excretion rates can still have a major impact if they are highly abundant and represent a significant portion of the total consumer biomass in the system (Hall et al. 2003, McIntyre et al. 2007). Assemblages with high abundances and biomass can have a strong indirect effect on the nutrient cycling process through other pathways such as bioturbation (Vaughn and Hakenkamp 2001), organic matter processing (Crowl et al. 2001b), and grazing (Pringle et al. 1999). Thus, the presence or absence of either a key single species or a dominant assemblage can determine the different pathways by which nutrients flow through the system, and losing these species could result in significant alterations to the nutrient cycles at the ecosystem-scale (Vaughn 2010, Whiles et al. 2013).

If consumers with significant roles in nutrient cycling are lost from the system, abiotic factors may become the principal factor regulating nutrient processes. Direct inputs of nutrients from the watershed, streamflow, and ambient concentrations influence the availability and movement of nutrient in stream ecosystems (Webster et al. 2003). However, the relative influence of these factors change over time as determined by temporal variation (Hoellein et al. 2007). Seasonal patterns of rainfall determine stream discharge and thus, the influence the input and export of dissolved nutrients in streams (McDowell and Asbury 1994, Peterson et al. 2001) This may also cause a temporary increase in nutrient background levels that could alter the cycling for a short time period (Peterson et al. 2001).

In small tropical streams both the presence of a key consumer and seasonal variation have proven key in regulating nutrients cycling processes (Benstead et al. 2010, Small et al. 2011). In this study, we assess the effects of losing a dominant consumer assemblage on reach-scale N (as NH4-N) and P (as PO_4^-) dynamics in tropical headwater streams of Puerto Rico. Our goals are: (1) to determine how nutrient processes change as a result of large-scale extirpations of a dominant consumer assemblage, and (2) to assess seasonal differences (high precipitation vs low precipitation seasons) in these dynamics. We estimated N and P uptake length, velocity, and rates in selected focal streams reaches across the island where migratory native macroconsumers have been absent for decades and compared these to streams where native stream communities remain unaltered. We also evaluated any differences in nutrient uptake rates between seasons (i.e. high precipitation season and low precipitation season) in order to identify any interactions between abiotic factors and the absence/loss of the native consumer assemblage. Due to the previously documented increase in benthic algae, organic matter, and inorganic matter in streams lacking native consumers above large dams (Greathouse et al. 2006c), we expect to find longer uptake lengths, lower uptake velocities, and lower uptake rates for both N and P in focal stream reaches above large dams compared to reaches without a downstream dam. We also expect shorter uptake length, higher uptake velocity, and higher uptake rate for both elements during the high precipitation season in streams above large dams. However, we do not expect a significant difference between seasons in undammed streams for any of the nutrient cycling parameters.

Methods

Study Sites

This study was conducted in high elevation headwaters streams across Puerto Rico. All stream reaches selected were located in forested areas within the central mountain region and El Yunque National Forest (hereafter EYNF) in the northeast region. Precipitation is relatively high year-round (annual average = 3500 mm) with periods of high rainfall between May and December, and low rainfall between January and April (Larsen 2000). Significantly high rain events can occur during both seasons but are more frequent during the high rainfall period resulting in relatively higher average discharge. Forested headwater streams in Puerto Rico are heavily shaded (canopy cover >80%) and have mixed substrates of bedrock, cobbles, sand, and pebbles. The stream gradient is very steep usually forming an ordered series of riffle and pool habitats with some high waterfalls (≥3 m) (Greathouse et al. 2006c, Covich et al. 2009). Allochthonous leaf and wood material are plentiful and represent an important habitat and energy source for the stream community.

Freshwater shrimps are the most dominant macroconsumers in terms of abundance and biomass in Puerto Rican streams. There are a total of seventeen species of native shrimps from three families (Atyidae, Xiphocarididae, and Palaemonidae) in the island (Perez-Reyes et al. 2013). The two most common and abundant genera are *Atya* (Atyidae, 3 species) and *Xiphocaris* (Xiphocarididae, 1 species), usually representing about 95% of the total assemblage (Covich and McDowell 1996). These two genera can reach combined densities of >20 individuals m^{-2} with the higher abundances occurring in high elevation reaches of the watershed (Covich et al. 2009). Both *Atya* and *Xiphocaris* are considered omnivorous and feed mostly on benthic algae and organic matter. When found in their normal high densities, shrimp assemblages regulate the levels of algae, benthic organic matter, and inorganic sediments through consumption and bioturbation (Pringle et al. 1993, Pringle et al. 1999, March et al. 2002, Cross et al. 2008b). Several studies have experimentally excluded shrimps from small areas of streams resulting in significantly higher levels of algae and both organic and inorganic matter, further proving that their strong top-down control regulate levels of algae, benthic organic matter, and benthic inorganic matter (Pringle and Blake 1994, Pringle et al. 1999, Greathouse et al. 2006b).

All of the native stream macrobiota (with the exception of the freshwater crab *Epilobocera sinuatifrons*) in Puerto Rico, including all shrimp species, are amphidromous. Large dams (wall > 15m) act as impermeable barriers that restrict their movement of all migratory consumers between the ocean and the headwaters, resulting in the complete extirpation of all shrimp species from streams above large dams without any connection to the downstream reaches (i.e. no spillway discharge, fish ladder, or water diversion around the reservoir) (Holmquist et al. 1998). About 27% of the total length of running waters in Puerto Rico are above large dams without a downstream connection, with the largest proportion of these being small headwater streams in the central mountainous region (Snyder et al. 2011). The loss of shrimp assemblages from these reaches has a significant effect on ecosystem properties at the landscape scale. Due to the lack of the strong shrimp top-down controls, levels of benthic algae, organic matter, and inorganic matter are significantly higher in streams above large dams where shrimp have been extirpated compared to undammed streams (Greathouse et al. 2006c).

We selected 6 focal stream reaches from across the island to conduct our experiments (Figure 4.1). Three of these streams were located upstream of a large dam (hereafter ‘dammed’) and the other 3 were selected from watersheds without any large dams (hereafter ‘undammed’). All dams below the focal reaches were constructed at least 30 years ago, providing sites where shrimp assemblages have been extirpated for decades (Table 4.1). We measured shrimp assemblage abundance and biomass once during each season at each stream. We deployed baited minnow traps at a density of 0.5 traps m^{-2} in five different pools across our study reaches. After leaving them in the streams for one night, we retrieved all traps, counted and measured all shrimps captured, and identified them to genus. Shrimp densities were estimated from total trap captures and sampling pool area (Covich et al. 2003). Biomass estimates were conducted for each taxa using available length-mass regressions (March 2000).

Nutrient uptake measurements

We estimated whole-reach uptake of N and P at each stream using the short-term addition method (Stream Solute Workshop 1990, Tank et al. 2007). We estimated uptake of both nutrients simultaneously by injecting a NH_4Cl and KH_2PO_4 solution. Our average target concentrations across all sites were 50 µg L^{-1} NH_4-N, and 40 µg L^{-1} soluble reactive phosphorus (SRP). We injected the mixed solution directly into the stream at a constant rate using a peristaltic pump (Fluid Metering Inc. model Q3CKC). Injection rates ranged from 35 to 50 mL min^{-1} and were determined independently for each replicate based on preliminary on-site estimates of stream discharge. We added chloride (dissolved NaCl) to the injection solution as a conservative tracer to calculate discharge during the injection and track saturation of the study reach using conductivity measurements. Length of study stream reaches ranged from 90 to 100 m across all sites (average = 96.6 ± 1.66 m; n=6). Each reach was divided into 5 stations starting about 20m downstream from the injection point to allow for mixing of the solution (Tank et al. 2007). Prior the addition we took a filtered (Millipore nitrocellulose pore size 0.45 µm) water sample at each station (n=5) to obtain background nutrient concentrations. We also measured conductivity at each station using a handheld conductivity meter (Hannah Instruments HI 9835N) to assess the baseline conductivity. We tracked changes in conductivity by constantly (every 30 seconds to 3 minutes) measuring it through the duration of the injections at the lowermost sampling station until it reached a steady state (plateau) which was our indicator of saturation for the reach. When the tracer reached plateau concentration, we took 3 more water samples at each station (n= 15). All water samples were stored in 60mL polyethylene bottles, placed on ice immediately after collection, and frozen within 12 hours. Water samples were analyzed for NH_4-N using the phenate-hypochlorite method, and for SRP using the ascorbic acid method (APHA 2005). All the analyses were performed at the Analytical Chemistry Lab at the University of Georgia (Athens, GA USA). Each injection was repeated 3 times during each season (high rain and low rain, n= 6 injections) at each stream (n= 36 total injections; 18 dammed and 18 undammed).

We estimated all of our nutrient dynamics parameters for both N and P using the exponential decay model:

$$\ln N_x = \ln N_0 - kx$$

where N_x is the nutrient concentration at plateau corrected for background, x is the distance downstream from the injection point, N_0 is the nutrient concentration at the injection point corrected for background and k is the decay rate (Stream Solute Workshop 1990). Uptake length (S_w; m) is obtained as the inverse of k:

$$S_w = k^{-1}$$

To account for variation in discharge between replicates we also estimated uptake velocity (V_f; m s^{-1}), as:

$$V_f = S_w (Q/w)$$

where Q is stream discharge (Ls^{-1}) and w is average stream width (m). We estimated areal uptake rates: (U; mg m^{-2} h^{-1}) as:

$$U = V_f N_b$$

where N_b is the nutrient background concentration of the stream. Areal uptake rate (hereafter ‘uptake rate’) provides the rate at which the inorganic nutrients in the water column are retained in the benthos. Although this method might not be the best to accurately estimate nutrient dynamics in streams, it has been supported as a proper way to establish comparisons between systems (Mulholland et al. 2002). Also, injecting both N and P simultaneously may relax limitation of the primary limited nutrient which could cause an increase in demand of the other (Benstead et al. 2010). These two limitations should not affect our study since our goal is to examine differences between streams and seasons.

Statistical analyses

We analyzed differences in uptake length, uptake velocity, and areal uptake between dammed and undammed streams reaches, and in between seasons using two-way ANOVAs. Each analysis was conducted twice independently for both N and P. Significant differences were further analyzed using post-hoc Tukey's Honest Significance Difference (HSD) tests. In cases where the *stream type x season* interaction effect was significant we analyzed the seasonal effect independently using t-tests. All statistical analyses were done using SAS (version 8.1, SAS Institute, Cary, NC).

We used published excretion values of two dominant genera of shrimps (*Atya* and *Xiphocaris*) in Puerto Rico from Benstead et al. (2010) to estimate total shrimp contribution of dissolved nutrients from excretion to nutrient demand. Using a similar approach to Griffiths and Hill (2014), we estimated total shrimp assemblage contribution from excretion as a function of the total biomass for both *Xiphocaris elongata* and *Atya spp.* Each estimate was done independently for each of the undammed streams. We compared this value to whole-reach uptake rates (U) to estimate the percentage of nutrients derived directly from shrimp excretion to calculate a percentage contribution of shrimp derived nutrients. We did this for both N and P during each season.

Results

Reach scale nutrient uptake

Mean physical and chemical parameters were similar between dammed and undammed streams during both study seasons (Table 4.2). Mean algal standing stock, fine benthic organic matter (FBOM), and fine benthic inorganic matter (FBIM) were higher in the dammed streams (Table 4.1). Means of all parameters measured changed between seasons but remained similar between dammed and undammed stream reaches. All nutrient uptake parameter estimates are summarized in Figure 4.2. None of the three measured N uptake parameters (uptake length: S_w, uptake velocity: V_f, uptake rate: U) had a significant factor interaction (stream type x season) effect ($p > 0.05$ for all 3) or differed significantly by season between dammed and undammed streams (S_w: $F_{1,32}$= 0.46 P= 0.52; V_f: $F_{1,32}$= 0.41, P= 0.53; U: $F_{1,32}$= 1.61, P= 0.21). Dammed streams during the high rain season had the longest N mean uptake length ($S_w = 94 \pm 2.40$ m), and undammed streams during the low rain season had the lowest ($S_w = 37.5 \pm 17.46$ m; Figure 4.2A) across the four possible rain/season combinations. Overall, uptake length of N was significantly longer during the high rain season for both dammed and undammed stream reaches ($F_{1,32}$= 11.21, P= 0.0021; Figure 4.2A), while mean N-uptake velocity (V_f) was significantly higher in both dammed and undammed streams during the low rain season ($F_{1,32}$= 6.363, P= 0.0168; Figure 2B). N uptake rates (U) did not differ significantly between seasons ($F_{1,32}$= 2.498, P= 0.1238; Figure 4.2C).

There was a significant interaction between stream reach type and season in P uptake length (S_w; $F_{1,32}$= 5.56, P= 0.02) and uptake velocity (V_f; $F_{1,32}$= 4.89, P= 0.03), so we analyzed those parameters independently. Mean P uptake length (S_w) was significantly higher during the high rain season (S_w = 83.66 ± 14.4) than during the low rain season (S_w = 32 ± 6) in undammed stream reaches (t= -3.42, P < 0.01; Figure 4.2D). There was no significant difference in P uptake length (S_w) between seasons in the dammed stream reaches (t= -0.19, P= 0.85; Figure 4.2D). Within season P uptake length (S_w) between dammed and undammed stream reaches also did not differ significantly for either the high rain season (t= -1.78, P= 0.09) or the low rain season (t= 1.54, P= 0.14; Figure 4.2D). Phosphorus uptake velocity (V_f) only differed significantly between seasons in the undammed streams, where P uptake velocity was significantly higher in low rain season (V_f = 0.14 ± 0.02 m s^{-1}) than in high rain season (V_f = 0.06 ± 0.04 m s^{-1}; t= 2.56, P= 0.02; Figure 4.2E). However, P uptake velocity (V_f) was not significantly different between seasons for the dammed streams (t= -0.74, P= 0.47; Figure 4.2E). There was no significant difference in uptake rate (U) of P between dammed and undammed streams ($F_{1,32}$= 0.33, P= 0.57; Figure 4.2F). Seasonal variation had a significant effect on P uptake rates. Phosphorus uptake rates were significantly higher in both dammed and undammed streams during the high rain season compared to the low rain season ($F_{1,32}$= 6.19, P= 0.02; Figure 4.2F).

Shrimps assemblages and excretion estimates

We did not find any shrimp in the three streams located above large dams. Total shrimp abundances and biomass were high in the three undammed streams (Table 4.3).

We found all three main families of shrimps in all of our streams without a large dam. However, our two focal taxa (*Atya* and *Xiphocaris*) corresponded to 91 % and 82 % of the total abundance and biomass respectively for the high rain season, and 92 % and 88 % of abundance and biomass for the low rain season. *Atya spp.* abundance ranged from 6.47 to 14.15 individuals m^{-2} during the high rain season (average = 8.36 ± 1.73 individuals m^{-2}), and from 5.72 to 11.87 (average = 7.66 ± 1.54 individuals m^{-2}) during the low rain season. *Xiphocaris* abundance ranged from 5.14 to 19.22 individuals m^{-2} during the high rain season (average = 13.11 ± 2.67 individuals m^{-2}) and from 9.77 to 22.11 (average = 19 individuals m^{-2}) during the low rain season. Total biomass for each taxon was proportional to its abundance (Table 4.3).

Estimates of the contributions of dissolved nutrients by shrimps to the reach scale uptake rates were very low. Estimated excretion rates averaged 13% (range: 10 - 17%; n=3; Figure 4.3) of the mean total N uptake rate during the high rain season, and 18% (range: 8 - 27%; n=3; Figure 4.3) during the low rain season. Estimates for P were substantially lower. During the high rain season, mean P derived from shrimp excretion contribute an average of 6% (range: 0.7 - 13%; n=3; Figure 3), and during the low rain season average contribution was only 3% (range: 0.5 - 6%; n=3; Figure 3).

Discussion

We compared the difference in N and P uptake parameters between dammed streams and undammed streams where shrimps are found in high densities. Our results suggest that losing shrimp assemblages did not have a strong effect on N cycling but did influence P cycling. Our uptake lengths for NH_4 are substantially longer than values previously reported from a ^{15}N tracer addition in streams in Puerto Rico (Merriam et al. 2002), however they are within the same range to the ones estimated by another study using our same method (Benstead et al. 2010). Seasonal variation seemed to be the main factor influencing nutrient cycling in our study. We also found significant differences in N and P uptake parameters between the low- and high-rain seasons in both the dammed and undammed streams.

Large dams and losing a dominant consumer

Although the differences in nutrient processing between dammed and undammed streams were not as strong as we expected, the extirpation of shrimp assemblages by dams did seem to have an effect. Phosphorus uptake length was shorter, and uptake velocity was higher in undammed streams. In these streams shrimps exert a strong top-down control on the epilithon keeping algae and benthic organic matter levels low (Pringle et al. 1999). This constant scraping and grazing of the benthic material could lead to an increase in autotrophic production thus increasing the demand for P. Although that grazing could have the opposite effect by removing the algae and thus reducing production and decreasing P demand (Mulholland et al. 1983), shrimps do not consume all the algae from the epilithon. As opposed to true grazers, shrimps are naturally omnivorous and their mouthparts are not adapted precisely to scrape the substrate clean of algae (Covich 1988). Thus, the level of grazing by shrimps should be ideal to promote higher primary production. This indirect consumer effect is completely absent from dammed streams. Algal standing stock, FBOM levels, and FBIM levels are very high when shrimps are found under very low densities or when they have been removed from the system (Pringle and Blake 1994, March et al. 2002). This same effect occurs at a larger scale in streams above large dams where shrimp have been completely extirpated (Greathouse et al. 2006c). Although we did not measure benthic primary production to directly quantify nutrient uptake associated with autotrophic production, we suggest that this process is the mechanism behind the difference in P uptake length and velocity between dammed and undammed streams.

However, we did not find the same result for Nitrogen. One possible explanation for the lack of difference in N uptake between dammed and undammed streams this could be lack of limitation due to short-term change in the background nutrient concentrations. Sanderson et al. (2009) showed that when background nutrient levels are relatively high the benthic community will take a lower percentage of the nutrient pool. It is possible that our lack of significant difference between dammed and undammed in N uptake parameters could be explained by the same principle. There are various ways in which shrimps themselves could increase the availability of N in the system. One example is their strong influence in the particulate organic matter decomposition process. Previous studies in Puerto Rico have shown that shrimps can significantly increase the decomposition rates of leaf litter material (March et al. 2001, Wright and Covich 2005, Crowl et al. 2006). This conversion of CPOM into smaller particles indirectly leads to a significant increase of N available in the water column, probably due to an increase in leaching rates (Crowl et al. 2001b). This is another function that is completely absent in streams above large dams that could compensate for a higher N demand. Besides shredding, shrimps could also resuspend significant levels of benthic material through bioturbation (Cross et al. 2008b). This could influence the amount of nutrients available in the water column in a similar way as the leaf decomposition, thus influencing nutrient cycling across the system. All this evidence suggests that shrimp indirect contribution to stream nutrient processes by bioturbation may exceed their direct effect through excretion (see below), and their indirect effect by consuming benthic algae and organic matter.

Shrimp direct contributions

Shrimp assemblages in the undammed sites were similar in terms of composition, abundance, and biomass to other previously reported in forested headwater streams of Puerto Rico (Covich et al. 1996, Covich et al. 2009, Perez-Reyes et al. 2013). Although shrimps appear to have an indirect effect on the nutrient cycling process by regulating benthic algae and FBOM (Pringle et al. 1993, Pringle et al. 1999, March et al. 2002, Greathouse et al. 2006b), our estimates suggest that they do not have a strong direct contribution through excretion. We estimated that shrimp excretion contributes of 21% of the N and 5% of the P (low rain season) of the measured nutrient uptake rate (U). These estimates are virtually identical to previous values reported for streams within EYNF (Benstead et al. 2010). Another important consideration is the proximity to the benthos of the resulting nutrients from shrimp excretion. Physical and hydrological parameters such as high discharge and depth reduce nutrient availability to the benthic community (e.g. high discharge). Shrimps spend most of the time feeding or resting on substrate so it is possible that shrimp-derived nutrients could be easier to obtain for the benthic microbiota, potentially increasing the importance of excretion-derived nutrients (Griffiths and Hill 2014).

It is possible that direct excretion by shrimps could be a significant contributor to the nutrient cycling in certain cases for our study streams. During drought conditions shrimp densities increase dramatically. The extremely low flows and decreased connectivity along the watershed restrict the shrimp movement and can isolate populations, which can result in densities of more than double of the regular assemblage (Covich et al. 2003). Under these conditions, the total contribution of dissolved nutrients from shrimp excretion could represent a higher percentage of the whole-reach demand.

Seasonal effects

Any potential effects from the shrimps, whether direct or indirect, could be affected by changes of the physicochemical or hydrological parameters. We found a significant stream x season interaction effect for uptake length (S_w) and velocity (V_f) of P. This interaction was driven by a significant difference in uptake length (S_w) and velocity (V_f) within the undammed streams, thus we looked at it independently. Higher uptake rate during the low rain season could be linked to the lower background concentrations measured for that season. Mean background SRP level was about 50% less. Dammed streams also experience that drop in background concentrations but their uptake parameters did not differ. We propose that the higher P uptake during the low rain season is associated with shrimp assemblages regulating benthic parameters. At stated above, top-down control of shrimps results in a low but stable level of algae maintaining primary production. Algae and FBOM did not differ significantly between seasons in these streams. Thus, a decrease in background levels while the P demand remained stable across season could have cause a seasonal P limitation. The same could be happening with N during the dry season.

Nitrogen also had a significantly higher uptake during the low rain season but in both the dammed and undammed streams. One factor that could be driving this difference in the dammed streams is the change in hydrologic parameters, particularly discharge. While dammed streams lack shrimps, the most important ecosystem regulator, discharge could potentially compensate for this loss. High discharge events have a substantial influence in benthic parameters by scouring of the benthic algae, organic matter, and sediments (Pringle and Hamazaki 1997). Also, uptake rates are generally related to discharge (Peterson et al. 2001). Even though we did not measure continuous discharge at our study site, we assumed that high rain events occurred more frequently during the high rain season as is normal for the whole island (Larsen 2000). Thus average discharge and stream depth would remain high during the high season, and changes in velocity and depth usually influence uptake length. Higher discharge and deeper habitats reduce the contact time between nutrients and the benthos and therefore reduce biotic uptake (Simon et al. 2005), which could be the factor driving the differences during the high rain season.

We acknowledge that nutrient cycling regulation by abiotic factors is very dynamic and hard to establish without precise data, especially for tropical streams. Parameters such as discharge and background nutrient concentration have a strong influence on nutrient cycling while at the same time are two of the most sensitive. Our goal was to capture the general picture of the factors that could be influencing nutrient dynamic in streams above large dams where shrimps have been extirpated.

Other scenarios

Large dams could have other significant effects that could be affecting the overall nutrient dynamics in Puerto Rican streams and rivers. One particular area that lacks information is looking at the importance of shrimp as a food and nutrient source for the rest of the aquatic community. Dams are blocking biomass and nutrients coming upstream, and shrimps in Puerto Rico are not site faithful so once the larvae reach the ocean they could return to any river (Cook et al. 2009) . Essentially, these shrimps that start their return trips on a dammed stream network run the possibility of climbing straight to a population sink. Many of these shrimps are consumed by predatory fish along the way (Agustin Engman *unpublished data*). Only a small percentage of shrimps that migrate upstream from the ocean eventually reach the high elevation streams (Kikkert et al. 2009). While we focus on the ecological effect of the shrimp extirpations through functional parameters, these assemblages per se could represent a large portion of the total amount nutrients not only in small headwater streams but also in complete drainage networks in Puerto Rico.

Another understudied aspect of how dams could alter nutrient processes is the role of exotic species. Holmquist et al. (1998) found that exotic fish species were significantly more abundant in streams above large dams where shrimps have been extirpated. Even though these fish cannot reach small streams in high elevation areas due to the presence of artificial and natural barriers (Cooney and Kwak 2013) their presence could still play an important role in nutrient cycling in downstream reaches. Capps and Flecker (2013) showed that high densities of an introduced aquarium fish (sailfin catfish; Loricariidae: Pterygoplichthys) in Mexico completely altered nutrient dynamics by acting as a P sink due to its high demand for the element. Moreover, grazing by this same species altered the quality of benthic resources (Capps and Flecker 2015) which could directly affect nutrient cycling by the epilithon (Dodds et al. 2004). This same genus of armored catfish has also been introduced in Puerto Rico (Kwak et al. 2007) and can be found in streams above large dams (PJ Torres personal observation). However their specific ecosystem level effects on streams in the island are still unknown.

Conclusions

Nutrient uptake parameters were substantially altered by large dams through the extirpation of shrimp assemblages. Our results highlight the importance of shrimp assemblages in regulating these processes. Although shrimp direct contribution to the nutrient cycle through excretion was low, their indirect effects by providing top-down control of benthic algae and organic matter (Greathouse et al. 2006c) proved to be one of the most important aspects in determining the differences in nutrient processes between dammed and undammed streams. However, abiotic factors can determine the relative contribution of shrimps at any given moment. In dammed streams, abiotic factors are practically the only force able to compensate for the loss of shrimp assemblages but they are not as stable.

References

Anderson, E. P., C. M. Pringle, and M. C. Freeman. 2008. Quantifying the extent of river fragmentation by hydropower dams in the Sarapiquí River Basin, Costa Rica. Aquatic Conservation: Marine and Freshwater Ecosystems 18:408-417.

APHA. 2005. Standard methods for the examination of water and wastewater. Washington, DC.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States. Page 308. North American Benthological Society.

Benstead, J. P., W. F. Cross, J. G. March, W. H. McDowell, A. Ramirez, and A. P. Covich. 2010. Biotic and abiotic controls on the ecosystem significance of consumer excretion in two contrasting tropical streams. Freshwater Biology 55:2047-2061.

Benstead, J. P., J. G. March, C. M. Pringle, and F. N. Scatena. 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. Ecological Applications 9:656-668.

Bukaveckas, P. A. 2007. Effects of channel restoration on water velocity, transient storage, and nutrient uptake in a channelized stream. Environ Sci Technol 41:1570-1576.

Capps, K. A., C. L. Atkinson, and A. T. Rugenski. 2015. Implications of species addition and decline for nutrient dynamics in fresh waters. Freshwater Science 34:485-496.

Capps, K. A., and A. S. Flecker. 2013. Invasive aquarium fish transform ecosystem nutrient dynamics. Proc Biol Sci 280:20131520.

Capps, K. A., and A. S. Flecker. 2015. High impact of low-trophic-position invaders: nonnative grazers alter the quality and quantity of basal food resources. Freshwater Science 34:784-796.

Chace, F. A., and H. H. Hobbs. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica [by] Fenner A. Chace, Jr., and Horton H. Hobbs, Jr. Washington, D.C. : Smithsonian Institution Press.

Connelly, S., C. M. Pringle, R. J. Bixby, R. Brenes, M. R. Whiles, K. R. Lips, S. Kilham, and A. D. Huryn. 2008. Changes in Stream Primary Producer Communities Resulting from Large-Scale Catastrophic Amphibian Declines: Can Small-Scale Experiments Predict Effects of Tadpole Loss? Ecosystems 11:1262-1276.

Cook, B. D., S. Bernays, C. M. Pringle, and J. M. Hughes. 2009. Marine dispersal determines the genetic population structure of migratory stream fauna of Puerto Rico: evidence for island-scale population recovery processes. Page 709.

Cooney, P. B., and T. J. Kwak. 2013. Spatial Extent and Dynamics of Dam Impacts on Tropical Island Freshwater Fish Assemblages. BioScience 63:176-190.

Covich, A., and W. H. McDowell. 1996. The Stream Community. Pages 434-459 *in* R. B. Waide and W. B. Reagan, editors. The food web of a tropical rainforest. University of Chicago Press, Chicago.

Covich, A. P. 1988. Geographical and Historical Comparisons of Neotropical Streams: Biotic Diversity and Detrital Processing in Highly Variable Habitats. Page 361. North American Benthological Society.

Covich, A. P., M. C. Austen, F. Barlocher, E. Chauvet, B. J. Cardinale, C. L. Biles, P. Inchausti, O. Dangles, M. Solan, M. O. Gessner, B. Statzner, and B. Moss. 2004. The role of Biodiversity in the functioning of freshwater and marine benthic ecosystems. BioScience 54:767-775.

Covich, A. P., T. A. Crowl, C. L. Hein, M. J. Townsend, and W. H. McDowell. 2009. Predator–prey interactions in river networks: comparing shrimp spatial refugia in two drainage basins. Freshwater Biology 54:450-465.

Covich, A. P., T. A. Crowl, S. L. Johnson, and M. Pyron. 1996. Distribution and abundance of tropical freshwater shrimp along a stream corridor: Response to disturbance. Biotropica 28:484-492.

Covich, A. P., T. A. Crowl, and F. N. Scatena. 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. Freshwater Biology 48:1199-1206.

Creed, R. P., R. P. Cherry, J. R. Pflaum, and C. J. Wood. 2009. Dominant species can produce a negative relationship between species diversity and ecosystem function. Oikos 118:723-732.

Cross, W. F., A. P. Covich, T. A. Crowl, J. P. Benstead, and A. Ramirez. 2008a. Secondary production, longevity and resource consumption rates of freshwater shrimps in two tropical streams with contrasting geomorphology and food web structure. Freshwater Biology 53:2504-2519.

Cross, W. F., A. Ramírez, A. Santana, and L. Silvestrini Santiago. 2008b. Toward Quantifying the Relative Importance of Invertebrate Consumption and Bioturbation in Puerto Rican Streams. Biotropica 40:477-484.

Crowl, T. A., N. Bouwes, M. J. Townsend, A. P. Covich, and F. N. Scatena. 2001a. Estimating the potential role of freshwater shrimp on an aquatic insect assemblage in a tropical headwater stream: a bioenergetics approach. International Association of Theoretical and Applied Limnology, Proceedings, Vol 27, Pt 4 27:2403-2407.

Crowl, T. A., W. H. McDowell, A. P. Covich, and S. L. Johnson. 2001b. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82:775-783.

Crowl, T. A., V. Welsh, T. Heartsill-Scalley, and A. P. Covich. 2006. Effects of different types of conditioning on rates of leaf-litter shredding by Xiphocaris elongata, a Neotropical freshwater shrimp. Journal of the North American Benthological Society 25:198-208.

Dodds, W. K., J. L. Tank, J. Pontius, S. K. Hamilton, N. B. Grimm, W. B. Bowden, W. H. McDowell, B. J. Peterson, H. M. Valett, J. R. Webster, and S. Gregory. 2004. Carbon and Nitrogen Stoichiometry and Nitrogen Cycling Rates in Streams. Page 458. Springer-Verlag.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews Of The Cambridge Philosophical Society 81:163-182.

Encalada, A. C., J. Calles, V. Ferreira, C. M. Canhoto, and M. A. S. Graca. 2010. Riparian land use and the relationship between the benthos and litter decomposition in tropical montane streams. Freshwater Biology 55:1719-1733.

Greathouse, E. A., J. G. March, and C. M. Pringle. 2005. Recovery of a tropical stream after a harvest-related chlorine poisoning event. Freshwater Biology 50:603-615.

Greathouse, E. A., C. M. Pringle, and J. G. Holmquist. 2006a. Conservation and management of migratory fauna: dams in tropical streams of Puerto Rico. Aquatic Conservation 16:695-712.

Greathouse, E. A., C. M. Pringle, and W. H. McDowell. 2006b. Do small-scale exclosure/enclosure experiments predict the effects of large-scale extirpation of freshwater migratory fauna? Oecologia 149:709-717.

Greathouse, E. A., C. M. Pringle, W. H. McDowell, and J. G. Holmquist. 2006c. Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico. Ecol Appl 16:339-352.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An Estimation of Historic and Current Levels of Salmon Production in the Northeast Pacific Ecosystem: Evidence of a Nutrient Deficit in the Freshwater Systems of the Pacific Northwest. Fisheries 25:15-21.

Griffiths, N. A., and W. R. Hill. 2014. Temporal Variation in the Importance of a Dominant Consumer to Stream Nutrient Cycling. Ecosystems 17:1169-1185.

Hall, R. O., J. L. Tank, and M. F. Dybdahl. 2003. Exotic Snails Dominate Nitrogen and Carbon Cycling in a Highly Productive Stream. Frontiers in Ecology and the Environment 1:407-411.

Hein, C. L., A. S. Pike, J. F. Blanco, A. P. Covich, F. N. Scatena, C. P. Hawkins, and T. A. Crowl. 2011. Effects of coupled natural and anthropogenic factors on the community structure of diadromous fish and shrimp species in tropical island streams. Freshwater Biology 56:1002-1015.

Helfield, J. M., and R. J. Naiman. 2001. Effects of Salmon-Derived Nitrogen on Riparian Forest Growth and Implications for Stream Productivity. Ecology:2403-2409.

Hoellein, T. J., J. L. Tank, E. J. Rosi-Marshall, S. A. Entrekin, and G. A. Lamberti. 2007. Controls on Spatial and Temporal Variation of Nutrient Uptake in Three Michigan Headwater Streams. Limnology & Oceanography 52:1964-1977.

Holmquist, J. G., J. M. Schmidt-Gengenbach, and B. B. Yoshioka. 1998. High dams and marine-freshwater linkages: Effects on native and introduced fauna in the Caribbean. Conservation Biology 12:621-630.

Hood, J. M., M. J. Vanni, and A. S. Flecker. 2005. Nutrient Recycling by Two Phosphorus-Rich Grazing Catfish: The Potential for Phosphorus-Limitation of Fish Growth. Page 247. Springer.

Johnson, P. T. J., J. D. Olden, and M. J. vander Zanden. 2008. Dam invaders: impoundments facilitate biological invasions into freshwaters. Frontiers in Ecology and the Environment 6:359-365.

Kaye, J. P., P. M. Groffman, N. B. Grimm, L. A. Baker, and R. V. Pouyat. 2006. A distinct urban biogeochemistry? Trends Ecol Evol 21:192-199.

Kikkert, D. A., T. A. Crowl, and A. P. Covich. 2009. Upstream migration of amphidromous shrimps in the Luquillo Experimental Forest, Puerto Rico: temporal patterns and environmental cues. Journal of the North American Benthological Society 28:233-246.

Kohler, A. E., A. Rugenski, and D. Taki. 2008. Stream food web response to a salmon carcass analogue addition in two central Idaho, U.S.A. streams. Freshwater Biology 53:446-460.

Kwak, T. J., P. B. Cooney, and C. H. Brown. 2007. Fishery population and habitat assessment in Puerto Rico streams: phase 1 final report. Federal Aid in Sport Fish Restoration Project F-50 Final Report, Submitted to Marine Resources Division, Puerto Rico Department of Natural and Environmental Resources, San Juan.

Larsen, M. C. 2000. Analysis of 20th century rainfall and streamflow to characterize drought and water resources in Puerto Rico. Physical Geography 21:494-521.

March, J. G. 2000. The role of freshwater shrimps : patterns and processes along a tropical island stream continuum, Puerto Rico University of Georgia, Athens, GA.

March, J. G., J. P. Benstead, C. M. Pringle, and M. W. Ruebel. 2001. Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. Canadian Journal of Fisheries & Aquatic Sciences 58:470.

March, J. G., J. P. Benstead, C. M. Pringle, and F. N. Scatena. 2003. Damming Tropical Island Streams: Problems, Solutions, and Alternatives. BioScience 53:1069-1078.

March, J. G., and C. M. Pringle. 2003. Food web structure and basal resource utilization along a tropical island stream continuum, Puerto Rico. Biotropica 35:84-93.

March, J. G., C. M. Pringle, M. J. Townsend, and A. I. Wilson. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. Freshwater Biology 47:377-390.

Marshall, M. C., A. J. Binderup, E. Zandona, S. Goutte, R. D. Bassar, R. W. El-Sabaawi, S. A. Thomas, A. S. Flecker, S. S. Kilham, D. N. Reznick, and C. M. Pringle. 2012. Effects of consumer interactions on benthic resources and ecosystem processes in a neotropical stream. Plos One 7:e45230.

Master, L. L., B. A. Stein, L. S. Kunter, and G. A. Hammerson. 2000. Vanishing assets: conservation status of U.S. species. Pages 93-118 *in* B. A. Stein, L. S. Kunter, and J. S. Adams, editors. Precious heritage: the status of biodiversity in the United States. Oxford University Press, New York.

McDowell, W. H., and C. E. Asbury. 1994. Export of Carbon, Nitrogen, and Major Ions from Three Tropical Montane Watersheds. Limnology and Oceanography 39:111-125.

McIntyre, P. B., L. E. Jones, A. S. Flecker, and M. J. Vanni. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. Proc Natl Acad Sci U S A 104:4461-4466.

McManamay, R. A., J. R. Webster, H. M. Valett, and C. A. Dolloff. 2011. Does diet influence consumer nutrient cycling? Macroinvertebrate and fish excretion in streams. Journal of the North American Benthological Society 30:84-102.

Merriam, J. L., W. H. McDowell, J. L. Tank, W. M. Wollheim, C. L. Crenshaw, and S. L. Johnson. 2002. Characterizing nitrogen dynamics, retention and transport in a tropical rainforest stream using an in situ 15N addition. Freshwater Biology 47:143-160.

Mitchell, N. L., and G. A. Lamberti. 2005. Responses in Dissolved Nutrients and Epilithon Abundance to Spawning Salmon in Southeast Alaska Streams. Limnology and Oceanography 50:217-227.

Mulholland, P., J. Tank, J. Webster, W. Bowden, W. Dodds, S. Gregory, N. Grimm, S. Hamilton, S. Johnson, and E. Martí. 2002. Can uptake length in streams be determined by nutrient addition experiments? Results from an interbiome comparison study. Journal of the North American Benthological Society 21:544-560.

Mulholland, P. J., A. M. Helton, G. C. Poole, R. O. Hall, S. K. Hamilton, B. J. Peterson, J. L. Tank, L. R. Ashkenas, L. W. Cooper, C. N. Dahm, W. K. Dodds, S. E. Findlay, S. V. Gregory, N. B. Grimm, S. L. Johnson, W. H. McDowell, J. L. Meyer, H. M. Valett, J. R. Webster, C. P. Arango, J. J. Beaulieu, M. J. Bernot, A. J. Burgin, C. L. Crenshaw, L. T. Johnson, B. R. Niederlehner, J. M. O'Brien, J. D. Potter, R. W. Sheibley, D. J. Sobota, and S. M. Thomas. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. Nature 452:202-205.

Mulholland, P. J., J. D. Newbold, J. W. Elwood, and C. L. Hom. 1983. The Effect of Grazing Intensity on Phosphorus Spiralling in Autotropic Streams. Page 358. Springer-Verlag.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific Salmon, Nutrients, and the Dynamics of Freshwater and Riparian Ecosystems. 5:399-417.

Perez-Reyes, O., T. A. Crowl, P. J. Hernandez-Garcia, R. Ledesma-Fuste, F. A. Villar-Fornes, and A. P. Covich. 2013. Freshwater decapods of Puerto Rico: a checklist and reports of new localities. Zootaxa 3717:329-344.

Peterson, B. J., W. M. Wollheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, E. Marti, W. B. Bowden, H. M. Valett, A. E. Hershey, W. H. McDowell, W. K. Dodds, S. K. Hamilton, S. Gregory, and D. D. Morrall. 2001. Control of Nitrogen Export from Watersheds by Headwater Streams. Science 292:86-90.

Pinay, G., J. C. Clément, and R. J. Naiman. 2002. Basic Principles and Ecological Consequences of Changing Water Regimes on Nitrogen Cycling in Fluvial Systems. Environmental Management 30:481-491.

Poff, N. L., and D. D. Hart. 2002. How Dams Vary and Why It Matters for the Emerging Science of Dam Removal. BioScience 52:659.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proc Natl Acad Sci U S A 104:5732-5737.

Pringle, C. M. 1996. Atyid shrimps (Decapoda: Atyidae) influence the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. Freshwater Biology 35:125.

Pringle, C. M., and G. A. Blake. 1994. Quantitative Effects of Atyid Shrimp (Decapoda, Atyidae) on the Depositional Environment in a Tropical Stream - Use of Electricity for Experimental Exclusion. Canadian Journal of Fisheries and Aquatic Sciences 51:1443-1450.

Pringle, C. M., G. A. Blake, A. P. Covich, K. M. Buzby, and A. Finley. 1993. Effects of Omnivorous Shrimp in a Montane Tropical Stream - Sediment Removal, Disturbance of Sessile Invertebrates and Enhancement of Understory Algal Biomass. Oecologia 93:1-11.

Pringle, C. M., and T. Hamazaki. 1997. Effects of fishes on algal response to storms in a tropical stream. Ecology 78:2432-2442.

Pringle, C. M., and T. Hamazaki. 1998. The Role of Omnivory in a Neotropical Stream: Separating Diurnal and Nocturnal Effects. Page 269. Ecological Society of America.

Pringle, C. M., N. Hemphill, W. H. McDowell, A. Bednarek, and J. G. March. 1999. Linking species and ecosystems: Different biotic assemblages cause interstream differences in organic matter. Ecology 80:1860-1872.

Ramirez, A., and L. R. Hernandez-Cruz. 2004. Aquatic insect assemblages in shrimp-dominated tropical streams, Puerto Rico. Biotropica 36:259-266.

Ranvestel, A. W., K. R. Lips, C. M. Pringle, M. R. Whiles, and R. J. Bixby. 2004. Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. Freshwater Biology 49:274-285.

Rincon, J., and A. Covich. 2014. Effects of insect and decapod exclusion and leaf litter species identity on breakdown rates in a tropical headwater stream. Rev Biol Trop 62 Suppl 2:143-154.

Rincón, J., and I. Martínez. 2006. Food Quality and Feeding Preferences of Phylloicus sp. (Trichoptera:Calamoceratidae). Page 209. North American Benthological Society.

Sanderson, B. L., H. J. Coe, C. D. Tran, K. H. Macneale, D. L. Harstad, and A. B. Goodwin. 2009. Nutrient limitation of periphyton in Idaho streams: results from nutrient diffusing substrate experiments. Page 832.

Simon, K. S., C. R. Townsend, B. J. F. Biggs, and W. B. Bowden. 2005. Temporal variation of N and P uptake in 2 New Zealand streams. Journal of the North American Benthological Society 24:1-18.

Simon, K. S., C. R. Townsend, B. J. F. Biggs, W. B. Bowden, and R. D. Frew. 2004. Habitat-Specific Nitrogen Dynamics in New Zealand Streams Containing Native or Invasive Fish. Page 777. Springer-Verlag.

Small, G. E., C. M. Pringle, M. Pyron, and J. H. Duff. 2011. Role of the fish Astyanax aeneus (Characidae) as a keystone nutrient recycler in low-nutrient Neotropical streams. Ecology 92:386-397.

Smith, G. C., A. P. Covich, and A. M. D. Brasher. 2003. An Ecological Perspective on the Biodiversity of Tropical Island Streams. Pages 1048-1051 BioScience.

Snyder, M. N., E. P. Anderson, and C. M. Pringle. 2011. A migratory shrimp's perspective on habitat fragmentation in the neotropics: extending our knowledge from Puerto Rico. Pages 169-182 *in* A. Asakura, editor. New Frontiers in Crustacean Biology: Proceedings of the TCS Summer Meeting, Tokyo, 20-24 September 2009. Koninklijke Brill NV, The Netherlands.

Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of Freshwater Ecosystems by Bivalves. BioScience 49:19.

Strayer, D. L., and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent progress and future challenges. Journal of the North American Benthological Society 29:344-358.

Stream Solute Workshop. 1990. Concepts and Methods for Assessing Solute Dynamics in Stream Ecosystems. Pages 95-118. North American Benthological Society.

Tank, J. L., M. J. Bernot, and E. J. Rosi-Marshall. 2007. Nitrogen limitation and uptake. Pages 213-238 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in Stream Ecology.

Taylor, B. W., A. S. Flecker, and R. O. Hall, Jr. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science 313:833-836.

Taylor, J. M., J. A. Back, T. W. Valenti, and R. S. King. 2012. Fish-mediated nutrient cycling and benthic microbial processes: can consumers influence stream nutrient cycling at multiple spatial scales? Freshwater Science 31:928-944.

Vanni, M. J. 2002. Nutrient Cycling by Animals in Freshwater Ecosystems. Annual Review of Ecology and Systematics:341-370.

Vanni, M. J., A. S. Flecker, J. M. Hood, and J. L. Headworth. 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. Ecology Letters 5:285-293.

Vaughn, C. C. 2010. Biodiversity Losses and Ecosystem Function in Freshwaters: Emerging Conclusions and Research Directions. BioScience 60:25-35.

Vaughn, C. C., and C. C. Hakenkamp. 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshwater Biology 46:1431-1446.

Webster, J. R., P. J. Mulholland, J. L. Tank, H. M. Valett, W. K. Dodds, B. J. Peterson, W. B. Bowden, C. N. Dahm, S. Findlay, S. V. Gregory, N. B. Grimm, S. K. Hamilton, S. L. Johnson, E. Martí, W. H. McDowell, J. L. Meyer, D. D. Morrall, S. A. Thomas, and W. M. Wollheim. 2003. Factors affecting ammonium uptake in streams – an inter-biome perspective. Freshwater Biology 48:1329-1352.

Whiles, M. R., R. O. Hall, W. K. Dodds, P. Verburg, A. D. Huryn, C. M. Pringle, K. R. Lips, S. S. Kilham, C. Colon-Gaud, A. T. Rugenski, S. Peterson, and S. Connelly. 2013. Disease-Driven Amphibian Declines Alter Ecosystem Processes in a Tropical Stream. Ecosystems 16:146-157.

Wold, A. K. F., and A. E. Hershey. 1999. Effects of salmon carcass decomposition on biofilm growth and wood decomposition. Canadian Journal of Fisheries and Aquatic Sciences 56:767-773.

Wright, M. S., and A. P. Covich. 2005. The Effect of Macroinvertebrate Exclusion on Leaf Breakdown Rates in a Tropical Headwater Stream. Biotropica 37:403-408.

Zeug, S. C., L. K. Albertson, H. Lenihan, J. Hardy, and B. Cardinale. 2011. Predictors of Chinook salmon extirpation in California's Central Valley. Fisheries Management and Ecology 18:61-71.

Tables

Table 4.1. General information of the study stream reaches used for the nitrogen and phosphorus additions.

Study Sites	Main Watershed	Stream Order	Elevation (m)	Downstream Dam	Dam construction year	Km above dam
Undammed						
(1) Caín	Guanajibo	2	323	NA	NA	NA
(2) Guayanilla	Guayanilla	1	450	NA	NA	NA
(3) Gatos	Espíritu Santo	2	510	NA	NA	NA
Dammed						
(4) Turabo	Grande de Loíza	2	310	Carraízo	1954	27
(5) Carite	La Plata	1	690	Carite	1913	5
(6) Limón	Jacagüas	1	487	Toa Vaca	1972	10

Table 4.2. Physicochemical characteristics of all study streams. Each value represents the mean (± 1SE) from three streams (N=3) from each stream type (dammed or undammed), during each season (high rain or low rain).

Parameters	High Rain Season				Low Rain Season			
	Dammed		Undammed		Dammed		Undammed	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Physical Parameters								
Discharge (Ls^2)	13	(±1.01)	17	(±2.16)	11	(±0.79)	15	(±1.56)
Width (m)	1.87	(±0.20)	1.83	(±0.13)	1.45	(±0.18)	1.7	(±0.33)
Depth (m)	0.15	(±0.04)	0.22	(±0.33)	0.10	(±0.02)	0.15	(±0.03)
Chemical Parameters								
Conductivity (µs cm^{-1})	345	(±26)	171	(±90)	289	(±111)	126	(±59)
NH$_4$ (µg L-1)	18.58	(±1.54)	16.73	(±2.09)	8.37	(±3.62)	10.39	(±2.13)
SRP (µg L-1)	17.43	(±3.21)	12.08	(±2.83)	6.44	(±1.14)	6.98	(±1.48)
Benthic Parameters								
Chlorophyll *a* (mg m^{-2})	10.23	(±4.349)	3.801	(±0.87)	10.786	(±3.397)	2.289	(±0.601)
AFDM (g m^{-2})	9.19	(±3.45)	2.98	(±1.67)	12.98	(± 9.81)	3.16	(±1.73)
Inorganic DM (g m^{-2})	34.23	(±12.34)	10.76	(±2.42)	27.76	(±16.77)	13.54	(±3.66)

Table 4.3. Shrimp abundance and biomass in the 3 undammed streams during the high and low rain seasons. Data represents mean (± 1SE) of three total night captures per site (n=9 each season).

Shrimp parameter and taxa	High rain season		Low rain season	
	Mean	SE	Mean	SE
Abundance (individuals m^{-2})				
Xiphocaris elongata	13.11	(±1.73)	11.23	(±1.88)
Atya spp.	8.36	(±0.52)	7.66	(±1.54)
Macrobrachium spp.	2.11	(±0.30)	1.7	(±0.43)
Biomass (g m^{-2})				
Xiphocaris elongata	19.39	(±4.67)	18.95	(±5.21)
Atya spp.	10.10	(±5.19)	11.66	(±3.99)
Macrobrachium spp.	4.25	(±0.19)	3.12	(±1.18)

Figures

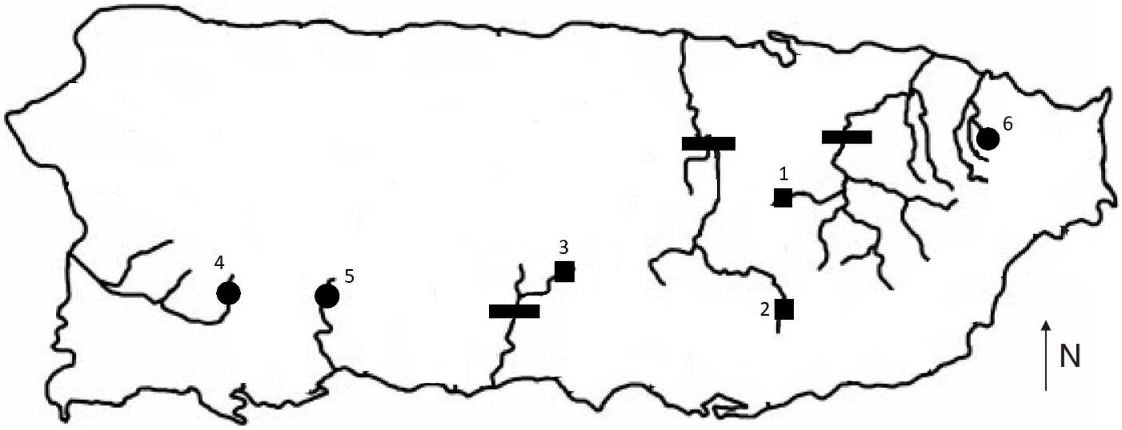

Figure 4.1: Map of Puerto Rico showing the six study site locations and their main drainage networks. Black bars represent dams, black squares represent our study sites on dammed streams (above dams), and black circles represent our study sites on undammed streams. Site numerical codes are referenced in Table 4.1.

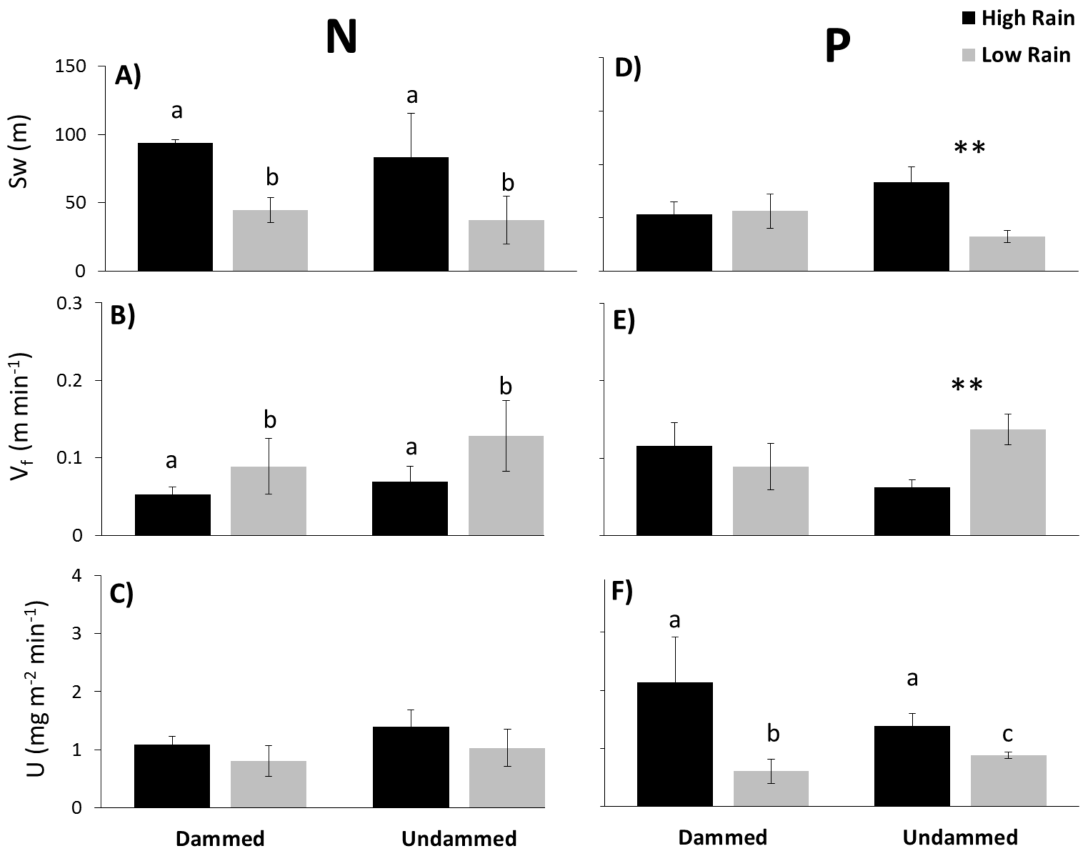

Figure 4.2. Summary of all N (A,B,C) and P (D,E,F) uptake parameters measured in dammed and undammed streams during the high rain (black bars) and low-rain (gray bars) seasons. Lowercase letters indicate groups that are significantly different based on Tukey's HSD following a significant ($p<0.05$) result from the two-way ANOVAs. Asterisks determine a significant *stream x season* interaction effect from the ANOVA followed by group independent t-tests and a significant difference ($p<0.05$) between the means within the group.

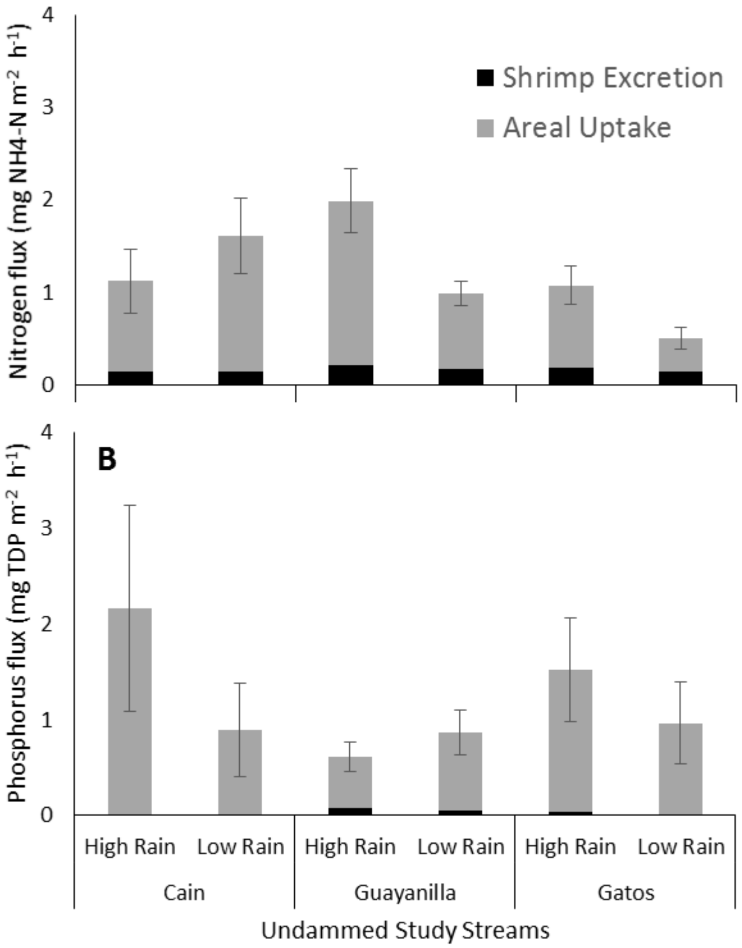

Figure 4.3. Reach-scale mean areal uptake (uptake rates, mg m^{-2} h^{-1}) and shrimp excretion estimates for all 3 undammed study streams during the high and low rain seasons. Shrimp excretion estimates were based from biomass measurements taken at the end of each nutrient addition experiment (n= 3 per season per site). Mass-excretion regressions for the same taxa were obtained from Benstead et al. (2010).

CHAPTER 5

CONCLUSION

Stream consumers are often linked to ecosystem-level properties and processes, and in tropical headwater streams of Puerto Rico, freshwater shrimps assemblages are an essential component for multiple ecosystem dynamics. Shrimps are the dominant consumer assemblage in Puerto Rican streams, usually present in high abundance and representing a significant portion of the ecosystem biomass (Covich and McDowell 1996). There are 18 species of freshwater shrimps from three different 13 families within the island (Xiphocarididae, Atyidae, and Palaemonidae) and all three families are usually represented in every free-flowing (undammed) high elevation stream (Perez-Reyes et al. 2013). Over the last four decades, plenty of studies have described specific roles of shrimp assemblages using reach-scale manipulative experiments. When present in their typical high abundance, shrimps are responsible for maintaining low levels of benthic algae (Pringle and Blake 1994), maintaining low levels of benthic organic matter (Pringle et al. 1999), clearing up benthic inorganic sediments (Cross et al. 2008), and keeping the nutrients flowing through the system (Crowl et al. 2001). The research presented here expands from this knowledge and provides a new broader dimension of the importance of shrimp assemblages within Puerto Rican streams.

I showed that landscape scale shrimp extirpations as a result of man-made dams (Holmquist et al. 1998) results in altered landscape patterns of leaf decomposition and nutrient cycling. Previous studies had documented evidence that large dams alter stream ecosystem properties through shrimp extirpations. High elevation headwater streams located upstream from large dams show higher algal standing stock, higher coarse benthic organic matter (CBOM) levels, higher fine benthic organic matter levels (FBOM), higher total benthic carbon and nitrogen (Greathouse et al. 2006). These results reemphasized what previous studies (mentioned above) have found in smaller scales. In this study (Chapters 2 and 3) I document, for the first time in Puerto Rico, that the dynamic aspect of the stream ecosystem (ecosystem processes) is also significantly affected by shrimp extirpations at the landscape scale.

Leaf litter decomposition is significantly reduced in the absence of shrimps and this pattern was persistent across all the dammed streams used for this study relative to the free-flowing undammed streams. A significant reduction in organic matter decomposition could result in altered energy flow across the food web and increased respiration rates in the ecosystem. Additionally, the absence of shrimps reduces the amount of organic matter that is transformed into living tissue, potentially increasing the overall quantity of particles flowing into reservoirs that could end up reducing their capacity and longevity.

Based on our findings, we suggest (1) that long-term monitoring effort continue but to expand these sampling efforts and increase the sampling frequency in order to better understand the influence of abiotic parameters over shorter interval periods in streams where the shrimps strong top-down control is not present. Additionally (2), ecosystem-level research efforts should consider the landscape perspective within entire watersheds to understand how landscape features, both natural and anthropogenic, ultimately determine consumer distribution and abundance, and therefore how stream ecosystem dynamics may be directly or indirectly affected by these altered

References

Covich, A., and W. H. McDowell. 1996. The Stream Community. Pages 434-459 *in* R. B. Waide and W. B. Reagan, editors. The food web of a tropical rainforest. University of Chicago Press, Chicago

Cross, W. F., A. Ramírez, A. Santana, and L. Silvestrini Santiago. 2008. Toward quantifying the relative importance of invertebrate consumption and bioturbation in Puerto Rican streams. Biotropica 40:477-484

Crowl, T. A., W. H. McDowell, A. P. Covich, and S. L. Johnson. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82:775-783.

Greathouse, E. A., C. M. Pringle, W. H. McDowell, and J. G. Holmquist. 2006b. Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico. Ecol Appl 16:339-352.

Holmquist, J. G., J. M. Schmidt-Gengenbach, and B. B. Yoshioka. 1998. High dams and marine-freshwater linkages: Effects on native and introduced fauna in the Caribbean. Conservation Biology 12:621-630.

Perez-Reyes, O., T. A. Crowl, P. J. Hernandez-Garcia, R. Ledesma-Fuste, F. A. Villar-Fornes, and A. P. Covich. 2013. Freshwater decapods of Puerto Rico: a checklist and reports of new localities. Zootaxa 3717:329-344.

Pringle, C. M., and G. A. Blake. 1994. Quantitative Effects of Atyid Shrimp (Decapoda, Atyidae) on the Depositional Environment in a Tropical Stream - Use of Electricity for Experimental Exclusion. Canadian Journal of Fisheries and Aquatic Sciences 51:1443-1450.

Pringle, C. M., N. Hemphill, W. H. McDowell, A. Bednarek, and J. G. March. 1999. Linking species and ecosystems: Different biotic assemblages cause interstream differences in organic matter. Ecology 80:1860-1872.