Secondary production, longevity and resource consumption rates of freshwater shrimps in two tropical streams with contrasting geomorphology and food web structure

WYATT F. CROSS*, ALAN P. COVICH*, TODD A. CROWL[†], JONATHAN P. BENSTEAD[‡] AND ALONSO RAMÍREZ[§]

Institute of Ecology, Odum School of Ecology, University of Georgia, Athens, GA 30602, U.S.A.
[†]*Ecology Center and Department of Aquatic, Watershed, and Earth Resources, Utah State, University, Logan, UT 84322, U.S.A.*
[‡]*Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, U.S.A.*
[§]*Institute for Tropical Ecosystem Studies, University of Puerto Rico, San Juan, Puerto Rico*

SUMMARY

1. Freshwater shrimps often dominate the biomass of tropical island streams and are known to have strong effects on stream ecosystem structure and function, but little effort has been dedicated toward quantifying basic energetic and life history attributes such as growth, production and longevity. Such information is critical for understanding both the role of shrimps in ecosystem dynamics and the gravity of threats to shrimp populations posed by human activities such as shrimp harvesting, dam construction and water withdrawal.

2. We quantified growth rates and secondary production of dominant freshwater shrimps for 3 years in two Puerto Rican headwater streams that differ in food web structure because of the presence or absence of predatory fishes that are excluded from reaches above waterfalls. Using growth data, we constructed a minimum longevity model to explore the likely minimum life spans of the two dominant taxa (*Atya* spp. and *Xiphocaris elongata*). Finally, we used a bioenergetics model to quantify annual consumption rates of major basal resources by the two taxa.

3. Daily growth rates ranged from −0.001 to 0.011 day^{-1}, were inversely related to body size, and were higher for small individuals of *X. elongata* than *Atya* spp. Mean annual shrimp biomass and secondary production were an order of magnitude higher in the stream that lacked predatory fishes (biomass: 4.34 g AFDM m^{-2}; production: 0.89 g AFDM m^{-2} year^{-1}) than in the stream with predatory fishes (biomass: 0.12 g AFDM m^{-2}; production: 0.02 g AFDM m^{-2} year^{-1}). Production : biomass ratios ranged from 0.01 to 0.38.

4. Our longevity model predicted a minimum life span of 8 years for *Atya* spp. and 5 years for *X. elongata* in the stream lacking predatory fishes. In contrast, due to a larger average size of *X. elongata* in the stream with predatory fishes, our model predicted a minimum life span of 11 years. Actual life spans of these taxa are likely to be much longer based on long-term observations of marked individuals.

5. Estimated consumption rates from the bioenergetics model indicated that *Atya* spp. and *X. elongata* are important processors of organic matter resources in streams where they occur at high densities. *Atya* spp. and *X. elongata* appeared capable of consuming a large proportion of algal and insect production and the proportion of direct leaf litter inputs consumed was also appreciable (*c.* 40–60%). However, the consumption of suspended fine particulate organic matter (SFPOM) by *Atya* spp. is probably only a minor proportion of total SFPOM flux in these streams.

6. Our study suggests that geomorphic features such as waterfalls may play an important role in controlling the distribution and production of freshwater shrimps through their effects on predatory fish movement. Spatial differences in shrimp densities result in landscape-scale variation in the significance to ecosystem processes of these long-lived organisms, particularly as processors of major organic matter resources.

Introduction

Freshwater shrimps often dominate biomass in tropical streams and rivers (e.g. Covich & McDowell, 1996; March *et al.*, 2002; Mantel & Dudgeon, 2004b; Greathouse & Pringle, 2006). Most of these taxa exhibit an amphidromous life history in which larvae released by gravid females drift passively to the estuary or ocean, grow into post-larvae and migrate upstream into freshwater for the remainder of their lives (Chace & Hobbs, 1969; March *et al.*, 1998; Benstead *et al.*, 1999; Fievet, 1999; Benstead, March & Pringle, 2000; Bauer, 2004). This migratory life history strategy exposes post-larvae to a number of natural and anthropogenic filters that may directly or indirectly alter their distribution and abundance in stream networks (Poff, 1997; Blanco & Scatena, 2006; Covich *et al.*, in press).

One landscape characteristic that appears to exert significant influence on shrimp abundance in head-water streams is the presence of large waterfalls. Such waterfalls limit the distribution of many predatory fishes, but do not represent a significant barrier for shrimps (Covich & McDowell, 1996; Pringle, 1997; Pringle *et al.*, 1999). Thus, shrimps that migrate above waterfalls may escape predation by fishes, and attain relatively high densities (Covich *et al.*, in press). Conversely, streams that lack large waterfalls contain populations of predatory fishes that may prevent shrimp from attaining high densities. Thus, food web structure in many tropical island streams may be governed by characteristics of landscape topography and geomorphology that influence the distribution of dominant predators. These landscape-level differences in shrimp abundance can have large effects on stream communities and ecosystem processes. For example, where abundant, shrimps can influence rates of leaf litter decomposition (e.g. March *et al.*, 2001; Crowl *et al.*, 2006), quantity and quality of epilithon and fine benthic organic matter (e.g. Pringle *et al.*, 1999; de Souza & Moulton, 2005; Greathouse *et al.*, 2006), heterogeneity of epilithic communities (Pringle, 1996) and fluvial export of dissolved and particulate nutrients (Crowl *et al.*, 2001). In addition, through feeding and bioturbation, shrimps can influence densities of other stream consumers, such as benthic insects (Pringle *et al.*, 1993; March *et al.*, 2002; Ramírez & Hernández-Cruz, 2004).

Despite the diverse ecological roles played by freshwater shrimps, as well as their widespread occurrence in tropical freshwater ecosystems, surprisingly few studies have quantified their basic energetic characteristics, such as growth rates and secondary production (but see Bright, 1982; Crowl *et al.*, 2000; Mantel & Dudgeon, 2004b; Yam & Dudgeon, 2005, 2006). In addition, with the exception of a vast literature (e.g. Jayachandran, 2001) on economically important aquaculture species (e.g. *Macrobrachium rosenbergii* [De Man]), relatively few studies have estimated the longevity and biomass replacement rates (i.e. production : biomass ratios) of freshwater shrimps. This information is critical for understanding the basic life history and bioenergetics of freshwater shrimps, the magnitude and variability of their effects on organic matter and nutrient processing in tropical streams (Crowl *et al.*, 2002), and the gravity of

potential threats posed by contemporary and future levels of human activities such as shrimp harvesting, dam construction and water withdrawal.

In this study, we quantified *in situ* growth rates, secondary production and biomass turnover rates of freshwater shrimps for 3 years in two tropical headwater streams that differed in geomorphology and also in food web structure because of the presence or absence of predatory fishes. We also constructed a minimum longevity model to explore the likely life span ranges of the dominant species. Lastly, we used a bioenergetics model to estimate the magnitude and long-term variation in organic matter consumption rates by shrimps in the two contrasting streams. Our results demonstrate potentially strong cascading effects of landscape geomorphology on secondary production and consumption by freshwater shrimps.

Methods

Study sites

This study was performed in two forest streams within El Yunque National Forest (formerly the Caribbean National Forest), Puerto Rico: Quebrada Prieta and Quebrada Bisley-3 (hereafter Prieta and Bisley). El Yunque is characterized as Tropical-Wet forest, and receives an average of 3.6 m of precipitation per year at mid-elevation where these streams are located. Long-term averages indicate that May through December is typically wetter than the rest of the year, but this seasonal pattern is highly variable. Both streams are first- to second-order and drain small, steep catchments. Large boulders and cobble dominate the stream substrata, leading to a series of pools interspersed with boulder-lined riffles; fine sediments and silt are present in depositional areas of pools and between large boulders. The streams are heavily shaded by a riparian forest community dominated by *Dacryodes excelsa* Vahl (tabonuco) and *Prestoea montana* (R. Grah) Nichols (sierra palm). Leaf fall is continuous throughout the year, but maxima and minima occur between April–June and December–March respectively (Zou *et al.*, 1995). Stream temperature is similar in both streams and ranges from 18 to 26 °C (mean: 22 °C). Discharge responds rapidly to local storm events, is highly variable and shows no major seasonal pattern. Both streams are relatively similar in physical and chemical characteristics and typical of other Caribbean island streams (http://luq.lternet.edu/data/; McDowell & Asbury, 1994; Covich *et al.*, in press).

Streams in El Yunque contain up to 10 species of freshwater shrimps, including four species of Atyidae (*Atya lanipes* Holthuis, *A. innocuous* [Herbst], *A. scabra* [Leach] and *Micratya poeyi* [Guérin-Méneville]), one species of Xiphocarididae (*Xiphocaris elongata* [Guérin-Méneville]) and five species of Palaemonidae (*Macrobrachium carcinus* [L.], *M. faustinum* [De Saussure], *M. crenulatum* Holthuis, *M. acanthurus* [Wiegmann] and *M. heterochirus* [Wiegmann]). The shrimp assemblage in Prieta is dominated by *X. elongata* and *A. lanipes* (>90% of individuals), while Bisley contains primarily *X. elongata*, *M. carcinus* and *M. faustinum*. All species are omnivorous, with dominant food sources largely determined by their prominent morphological features. *Xiphocaris elongata* have tiny pincers that are used to shred leaf litter, collect fine particles or periphyton, and capture insect prey. All atyids have modified cheliped fans that they use to filter seston or scrub fine benthic particles (Covich, 1988; Bauer, 2004). Palaemonids (*Macrobrachium* spp.) tend to be more predatory (March & Pringle, 2003; Mantel & Dudgeon, 2004a) than other shrimps in these streams, but also probably consume algal and detrital basal resources (March & Pringle, 2003).

Predatory fish are absent from Prieta, due to a large waterfall downstream that prevents their upstream dispersal. In contrast, predatory fishes (predominantly mountain mullet [Mugilidae: *Agonostomus monticola* (Bancroft)] and American eel [Anguillidae: *Anguilla rostrata* (Le Seur)]) are relatively abundant in Bisley where there is no major barrier to upstream migration (Townsend *et al.*, 2002; Covich *et al.*, in press).

Growth rates

Daily growth rates (mg mg^{-1} day^{-1}) of shrimps were determined for a broad range of size-classes using two methods. For mid-to large-sized shrimps, we quantified growth rates of tagged individuals *in situ*. Between December 2004 and March 2005, approximately 500 *A. lanipes* [≥8.6 mm orbital carapace length, (OCL)] and *X. elongata* (≥7.7 mm OCL) were collected from Prieta, measured under a dissecting microscope (OCL to the nearest 0.1 mm), tagged with uniquely coded Soft Visible Implant Alphanumeric

tags (VIalpha; Northwest Marine Technologies, Shaw Island, WA, U.S.A.), and released back into the stream within 24–48 h of collection. After a sufficient time period (60–280 days) tagged shrimps were recaptured and measured as above. Previous research has shown that these tags do not significantly affect growth rates of freshwater shrimps (e.g. Mantel & Dudgeon, 2004b); however, we did not assess this source of uncertainty in our study. For smaller-sized individuals, which are difficult to tag and recapture, we quantified growth rates in nine flow-through stream-side channels (individual channel dimensions: 2.4 × 0.23 × 0.20 m; channels were constructed with wood and PVC pond liner; each channel was covered with shade cloth) at the El Verde Field Station in the Luquillo Experimental Forest. Multiple *A. lanipes*, *X. elongata* or *Macrobrachium* spp. were collected from streams near the El Verde Field Station, sorted into size-classes of 1-mm intervals, and placed in separate stream-side channels. Each channel received a continuous supply of stream water and fine particles from a small stream adjacent to the field station. Conditioned leaf litter collected from the adjacent stream was also added to the channels at monthly intervals. Water temperature in the channels (mean: 20 °C) was similar to that of the adjacent stream, as well as Prieta (mean: 22.2 °C; range 17.9–24.2; measured between 22 June 2005 and 24 February 2006). All shrimps were measured as above before and after the incubations (ranged 70–180 days). Biomass of individuals was calculated using previously established OCL-weight (ash-free dry mass, AFDM) relationships (Greathouse, 2005). Daily growth rates (day^{-1}) were calculated as g = (lnM_f − lnM_i)/t, where M_f is the final AFDM of individuals or the average final AFDM of size-classes, M_i is the initial AFDM of individuals or the average initial AFDM of size-classes and *t* is the length of time (days) between the initial and final measurements. Relationships between growth rates and initial size were examined with regression analysis.

Abundance, biomass and secondary production

Shrimps were sampled quantitatively in Prieta and Bisley in 2003, 2004 and 2005 (Covich *et al.*, 1991; Covich, Crowl & Scatena, 2003) as part of the Long-Term Ecological Research monitoring programme at the Luquillo Experimental Forest. At least twice each year, shrimps were sampled from six pools along the length of each stream using wire minnow traps baited with dry cat food (mesh size: 0.36 cm^2) at a density of approximately 0.5 traps per square metre. Traps were deployed in the afternoon, left overnight and collected the following day. Upon collection, shrimps were identified, counted, their carapace length measured with calipers (nearest 0.1 mm; total carpace length measured in 2003 and 2004, orbital carpace length measured in 2005), and returned to the same pool. To standardize lengths among years, we converted total carapace length to OCL using linear equations based on 25–30 individuals across a wide range of body size. Length and width of each pool at multiple cross sections were measured to quantify pool surface area and calculate shrimp abundance and biomass on an areal basis.

During each sampling date at each pool, only a fraction (generally the first 100–150) of the shrimp carapace lengths was measured. Thus, to calculate the distribution of biomass among size-classes, we constructed size-frequency histograms for each pool. The proportions of shrimps in each 1-mm size-class were then multiplied by the total abundance in the pool to calculate the predicted total biomass in each size-class.

Our sampling method assumes that trapped shrimps came only from the pool that was sampled, and that all individuals in the pool were caught in the traps. However, this method probably underestimates total abundance because individuals that are smaller than the mesh size can freely move in and out of the traps. In an effort to account for this discrepancy, we sampled shrimps in Prieta on two dates during 2004–05 in six locations (three pools and three riffles) using a pass-depletion method. Pass depletion uses observed declines in abundance over multiple removals from the same habitat to obtain an estimate of actual total abundance (Zippin, 1958). We compared size frequency histograms from pass depletions to those from trap data to approximate the proportion of shrimp biomass and production not accounted for by the wire traps, and to examine potential bias introduced by trap sampling. Due to low shrimp densities, this approach was not feasible in Bisley.

We used a bootstrap-resampling technique (Manly, 2001) to estimate uncertainty associated with measures of population abundance, biomass, and secondary production. For each species on each sampling

date, abundance data from the six pools were resampled with replacement to generate 1000 estimates of mean abundance. This process was repeated for each date and the values for multiple dates were averaged to get 1000 estimates of mean annual abundance. From these data, we calculated a grand mean and 95% confidence limits (Efron, 1979). A similar resampling technique was used to estimate mean biomass for each 1-mm interval size-class of shrimp. These size-specific biomass estimates were then summed to get 1000 estimates of total biomass. A grand mean and 95% confidence limits were again calculated from these data.

Secondary production was calculated for each size-class using the instantaneous growth method (Benke & Huryn, 2006). Size-specific growth rates for each taxonomic group (i.e. *Atya* spp., *X. elongata*) were resampled to generate 1000 equations relating initial size and growth rate. The slopes and intercepts of these equations were first used to generate 1000 growth rate estimates for a given size-class. Next, estimates of annual secondary production for each size-class were generated by multiplying growth estimates by the 1000 biomass estimates and 365 days. Mean annual production and 95% confidence intervals were then calculated from these data. Negative growth rate values were not included for production estimates. This method assumes that size-specific growth rates are similar throughout the year because of minimal variation in stream temperature.

Our secondary production estimates require a few caveats. First, our growth rates for *Macrobrachium* spp. were limited, and largely restricted to small individuals grown in stream-side channels. For this reason, we estimated production of *Macrobrachium* spp. using a general growth equation derived from all species combined. Secondly, we used growth estimates from Prieta and the stream-side channels to calculate production of shrimp in Bisley. Thus, any differences between these streams that may affect growth (e.g. food quality, predation pressure) would influence our estimates of production. However, as shown below, variation in production of these slow growing taxa is largely driven by variation in biomass, not individual growth rates. Lastly, we did not include losses of biomass to molting in our production estimates, which can be substantial for decapods (up to 25% at each molt, Huryn & Wallace, 1987).

Longevity

To estimate the likely life spans of the dominant shrimp species (i.e. *Atya* spp. and *X. elongata*), we constructed a minimum longevity model (based on Huryn, Koebel & Benke, 1994). The model was initiated with individuals at 5 mm OCL (i.e. no initial size variability), assumed to be roughly equivalent to 1 year after hatching. On a daily basis, the model approximated the growth rates (and uncertainty therein) of 1000 individuals using the full bootstrapped range in slope and intercept values from our data relating initial size to growth rate. This process was repeated iteratively until individuals reached the size at which growth was negligible (generally 12–13 years). At the end of each year, we calculated the bootstrapped 95% confidence limits of OCL for all individuals. We then compared our model output to the size of the largest individuals observed, as well as the body size that included 99% of our observations throughout the study.

Consumption rates

To estimate areal consumption rates, we constructed a shrimp bioenergetics model for the two dominant taxa in our study streams (*Atya* spp. and *X. elongata*) using a standard software application (Fish Bioenergetics 3.0; Hanson *et al.*, 1997). Few physiological data are available for these taxa, so the model was parameterized using literature values from physiologically similar shrimp species (see Table 1). For the same reason, the basic model was used for both *Atya* spp. and *X. elongata* consumption. Model input for the two taxa differed only in the taxon-specific growth data obtained in the field, as well as the relative contributions of resource categories to their diets (Table 2). Detailed diet data were not available, so diet contributions were estimated based on limited observations of gut contents and the authors' knowledge of species biology. Although diet proportions obviously affect estimated relative consumption of diet categories, model output is constrained by many other parameters (see Table 1). Our estimates of total consumption are therefore relatively robust to error in diet proportions.

Estimating consumption rates using the bioenergetics model involved the following steps. First, we calculated annual growth increments [g wet mass (WM)] for 1-mm interval size-classes of each species using growth rates from the Prieta stream (see Fig. 1).

Table 1 Values of parameters used in the bioenergetics model used to calculate consumption by *Atya lanipes* and *Xiphocaris elongata*, with symbols, equations used from the bioenergetics model (Hanson *et al.*, 1997) and literature sources for parameter values

Budget component	Symbol	Parameter	Source
Consumption (equation 1)			
Allometric function intercept	CA	0.09	Franco *et al.* (2006)
Allometric function slope	CB	−0.38	Franco *et al.* (2006)
Temperature coefficient	CQ	0.1	Hanson *et al.* (1997)
Respiration (equation 2)			
Optimum temperature (°C)	RTO	28	Authors' estimate
Maximum temperature (°C)	RTM	35	Authors' estimate
Q_{10} over low temperatures (°C^{-1})	RQ	2.4	Iwasa & Miura (1976)
Allometric function intercept	RA	0.01	Iwasa & Miura (1976)
Allometric function slope	RB	−0.38	Iwasa & Miura (1976)
Activity multiplier	ACT	2	Winberg (1956)
Specific dynamic action	SDA	0.18	Rudstam (1989)
Egestion/excretion (equation 1)			
Proportion of energy egested	FA	0.15	Rudstam (1989)
Proportion of energy lost as excretion	UA	0.18	Rudstam (1989)

Table 2 Proportions of diet categories used in bioenergetics modelling of consumption by *Atya lanipes* and *Xiphocaris elongata*, with energetic equivalents and per cent water content

Diet category	Proportion*	Energetic equivalent J g^{-1} WM^2	% Water[†]
Atya lanipes			
Leaf litter	0.15	1118	15
SFPOM	0.6	1200	20
Periphyton	0.25	3189	80
Xiphocaris elongata			
Leaf litter	0.4	1118	15
Periphyton	0.55	3189	80
Insects	0.05	4698	80

SFPOM, suspended fine particulate organic matter.
*Authors' estimates.
[†]Cummins & Wuycheck (1971).

Based on these growth increments, we then used the model to calculate annual consumption of each resource category by an individual in each size-class of each species. Finally, we multiplied consumption of each resource category by the density of the respective size-class of each species in the two streams. Size-class frequency distributions and abundances were obtained from the long-term trapping data available for each stream (Figs 2 & 3).

We applied this approach to examine both spatial and temporal differences in consumption rates of these two dominant taxa on a per-area basis. First, we compared mean areal consumption rates of *Atya* spp. and *X. elongata* in Prieta and Bisley over 3 years (2003–05). Secondly, we used a 16-year record of abundances (1990–2005) in a single pool in the Prieta stream to examine long-term variability in the areal impact of

these two taxa on their resources. This record is long enough to incorporate the effect of occasional large disturbances on densities (e.g. hurricanes; Scatena & Larsen, 1991). For all bioenergetics modelling, we assumed that water temperature was a constant 22 °C in both the Prieta and Bisley streams (W.F. Cross, unpubl. data). We also assumed that shrimp biomass was 75% water with a constant energetic equivalent of 4700 J g^{-1} WM (Cummins & Wuycheck, 1971).

Results

Growth rates

Growth rates of both *Atya* spp. and *X. elongata* in Prieta ranged from −0.001 to 0.011 mg mg^{-1} day^{-1} (Fig. 1). Maximum growth rates of *X. elongata* were more than double those of *Atya* spp, but these differences were only apparent for smaller individuals. Initial size (OCL) was a rather good predictor of individual growth rates, explaining between 46% and 57% of the variation (Fig. 1). Growth rates declined strongly with body size, and growth was at or near zero above 11 mm OCL for *X. elongata* and 8 mm for *Atya* spp. Limited measurements of *Macrobrachium* spp. growth rates (four individuals not shown) ranged from 0 to 0.0063 (OCL ranged 3.5–14.9).

Size structure

Size-frequency histograms of *X. elongata* and *Atya* spp. based on long-term monitoring data from Prieta did not differ qualitatively across sampling dates within a
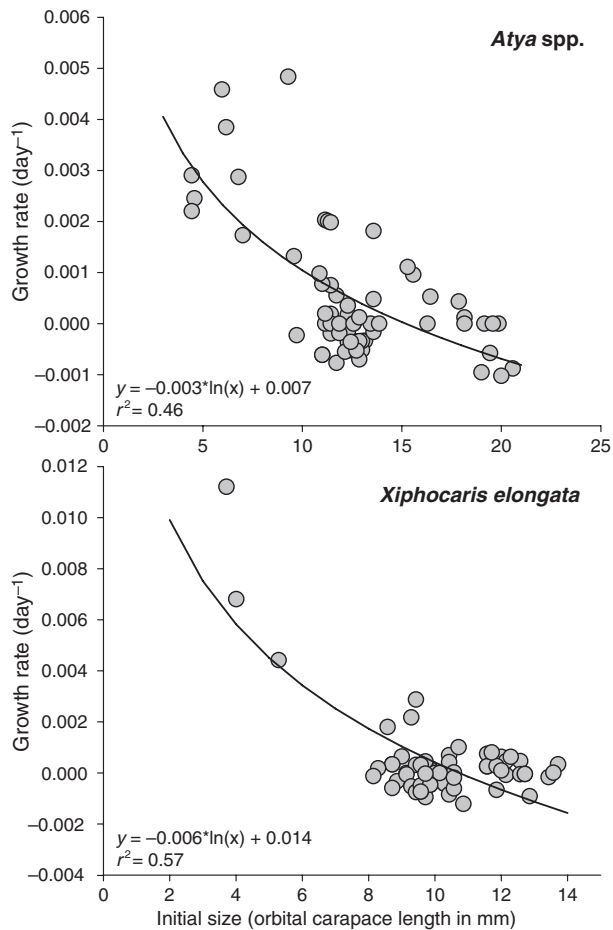
Fig. 1 Relationships between initial orbital carapace length (mm) and instantaneous growth rates (day^{-1}) of *Atya* spp. and *Xiphocaris elongata*. Growth rates were quantified from tagged individuals *in situ* and in stream-side channels.

year (*n* = 2–3 per year) or across years (*n* = 3). Size-frequency distributions of *Atya* spp. (predominantly *A. lanipes*) were bimodal with peaks at 12 and 18 mm OCL (Fig. 2a). Sizes of *X. elongata* were more normally distributed, with most individuals between 9 and 10 mm OCL (median 9.5 mm OCL; average 11.0 mm OCL; Fig. 2c).

Histograms constructed from pass-depletion sampling in 2004–05 differed from the long-term histograms (Fig. 2b,d). A large percentage (46%) of *Atya* spp. individuals were small and ranged from 5 to 8 mm OCL. Differences between long-term and pass-depletion estimates were not as apparent for *X. elongata*, but sizes from pass-depletion estimates were slightly skewed towards smaller individuals (Fig. 2c,d).

A size-frequency histogram of *X. elongata* in Bisley (based on 2003 and 2004 data) showed that most

individuals were considerably larger than in Prieta (Fig. 2e). Histograms of *Macrobrachium* spp. are not shown for Prieta or Bisley because of an extremely broad size range and no apparent pattern.

Abundance, biomass and secondary production

Total shrimp density in Prieta averaged 14.5 m^{-2} across all 3 years of the study, of which *Atya* spp. and *X. elongata* constituted 8.5 and 6.0 m^{-2}, respectively (Fig. 3). Densities of *Macrobrachium* spp. were extremely low in Prieta, averaging 0.08 m^{-2}. Shrimp densities in Bisley were almost two orders of magnitude lower than Prieta, and were evenly split between *X. elongata* (0.15 m^{-2}) and *Macrobrachium* spp. (0.14 m^{-2}; Fig. 3). *Atya* spp. were never collected in Bisley with the minnow traps.

Mean annual shrimp biomass in Prieta averaged 4.34 g AFDM m^{-2} (*Atya* spp. 3.07 g AFDM m^{-2}; *X. elongata* 1.21 g AFDM m^{-2}; *Macrobrachium* spp. 0.07 g AFDM m^{-2}). Mean annual biomass in Bisley was much lower than Prieta, averaging 0.12 g AFDM m^{-2} (*X. elongata* 0.06 g AFDM m^{-2}; *Macrobrachium* spp. 0.06 g AFDM m^{-2}). Mean annual shrimp production in Prieta averaged 0.89 g AFDM m^{-2} year^{-1} (*Atya* spp. 0.53 g AFDM m^{-2} year^{-1}; *X. elongata* 0.33 g AFDM m^{-2} year^{-1}; *Macrobrachium* spp. 0.02 g AFDM m^{-2} year^{-1}). Annual shrimp production in Bisley averaged 0.02 g AFDM m^{-2} year^{-1}, of which *Macrobrachium* spp. almost completely dominated (0.019 g AFDM m^{-2} year^{-1}).

Production to biomass (P : B) ratios were consistently low among taxa and years (range 0.01–0.38; Fig. 3). Extreme low P : B ratios for *X. elongata* in Bisley resulted from large average size of individuals, low individual growth rates and consequent low secondary production. Average P : B ratios between 0.1 and 0.4 translate to biomass replacement times of 2.5–10 years. Large overlap of bootstrapped 95% confidence limits indicated minimal inter-annual variability in shrimp abundance, biomass, and production (Fig. 3). *Atya* spp. abundance, biomass and production were lower during 2004 than 2003.

Longevity

Our longevity model predicted a minimum life span of *c.* 8 years for *Atya* spp. and 5 years for *X. elongata* in Prieta (estimated from the point at which the upper
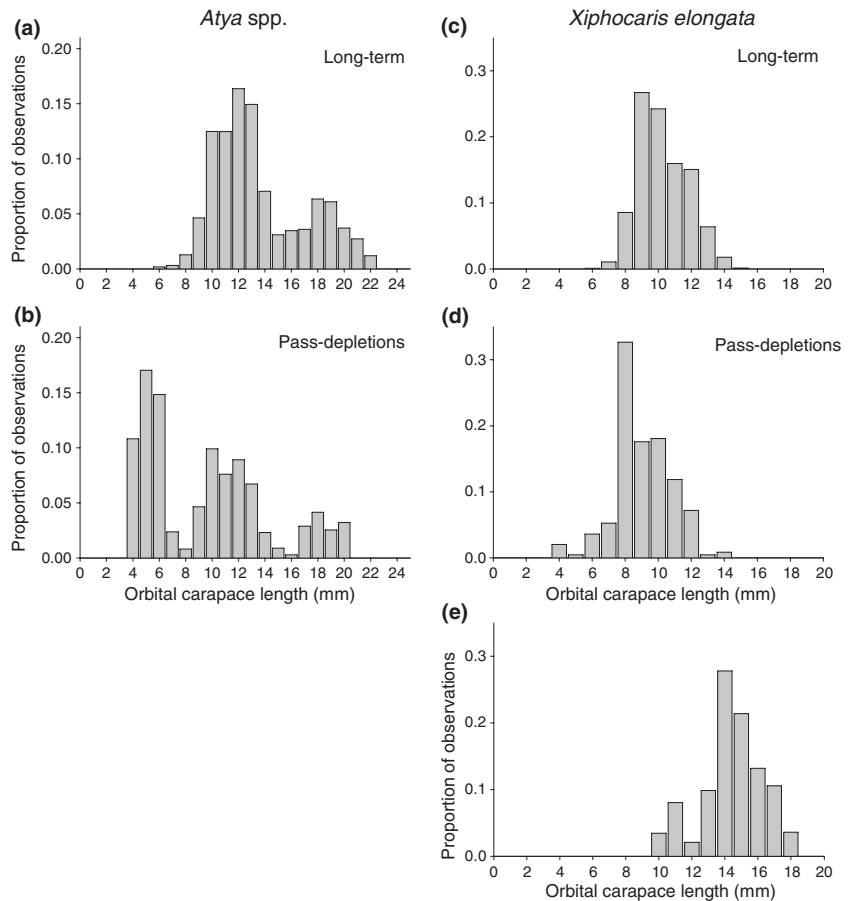
Fig. 2 Size-frequency histograms of *Atya* spp. and *Xiphocaris elongata* from long-term wire trap collections (a, c) and from pass-depletions in 2004–05 (b, d) in Quebrada Prieta. Panel 'e' shows the size frequency histogram for *Xiphocaris elongata* in Quebrada Bisley.

confidence limit overlaps the size that included 99% of individuals in this study; Fig. 4). Because *X. elongata* were considerably larger in Bisley, their minimum life span was predicted to be 11 years (Fig. 4). The maximum sizes observed for *Atya* spp. and *X. elongata* in both streams were not considerably larger than the size threshold that included 99% of individuals observed.

Consumption

The proportion of maximum consumption rate in the model ranged from 0.28 to 0.3 among size-classes of *Atya* spp. Gross production efficiency (GPE; g WM growth increment divided by total g WM consumed) ranged from 1.6% to 0%. Consumption by *Atya* spp. in Prieta was dominated by large amounts of suspended fine particulate organic matter (SFPOM; >1200 g DM m^{-2} in some years; Fig. 5 & Table 3). Leaf litter and periphyton were also significant resources for *Atya* spp., with typical annual consumption rates of 150 and

75 g DM m^{-2}, respectively (Fig. 5 & Table 3). For *X. elongata*, the proportion of maximum consumption rate ranged from 0.19 to 0.21 among size-classes. GPE ranged from 2.2% to 0%. Consumption by *X. elongata* differed in being lower that those by *Atya* spp. and in being dominated by leaf litter, with periphyton and insects less important. Low densities of *X. elongata* and the virtual absence of *Atya* spp. in the Bisley stream resulted in consumption estimates that were two orders of magnitude lower than those estimated for the Prieta stream (Table 3). The 16-year record from Pool 0 in the Prieta stream revealed large shifts in consumption rates driven by temporal changes in abundance of the two species (Fig. 5). Both *Atya* spp. and *X. elongata* showed two- to threefold differences in consumption rates over this long-term record (Fig. 5).

Discussion

In northeastern Puerto Rico, like many tropical islands, rugged landscapes with large changes in
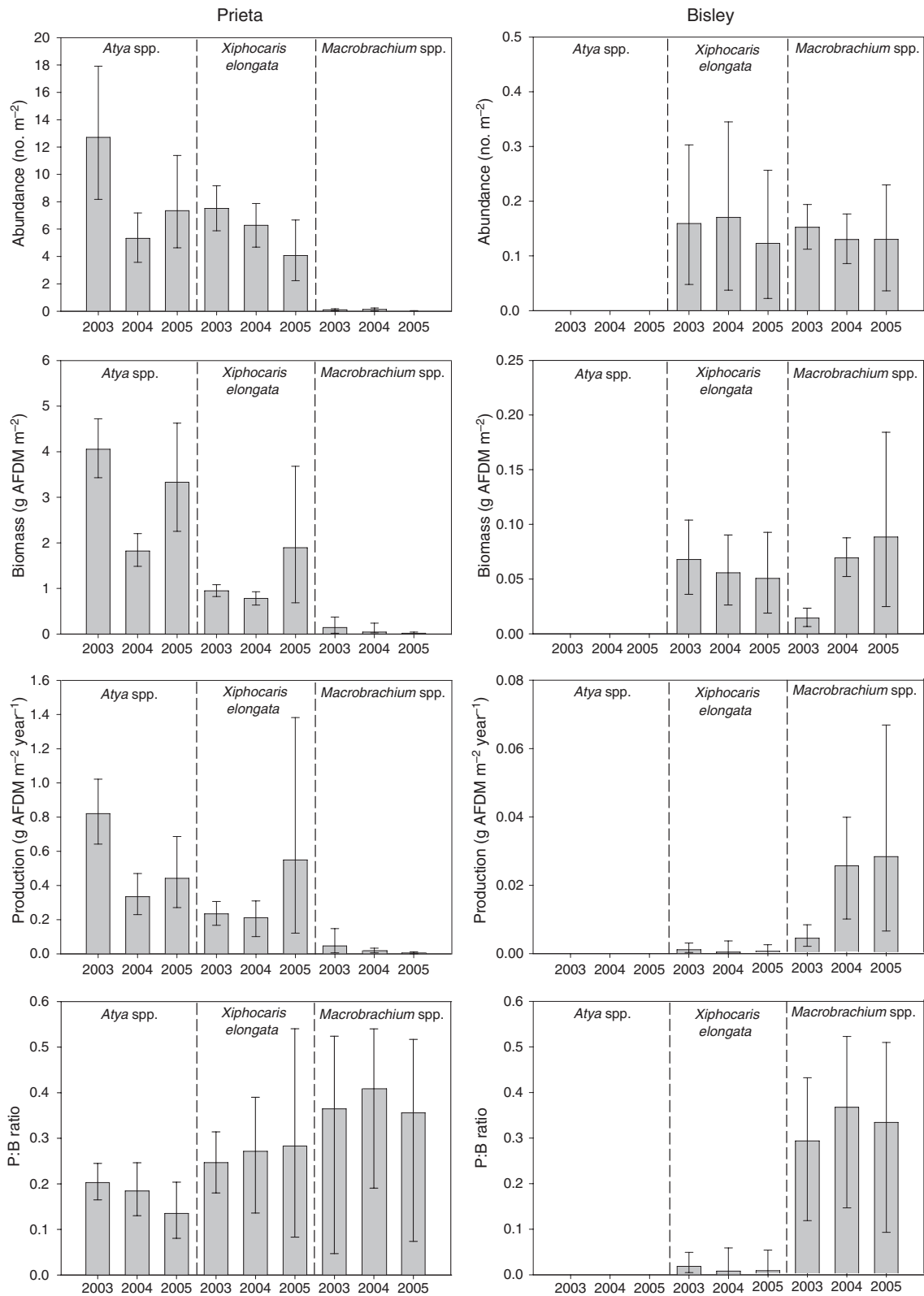
Fig. 3 Mean annual (2003–05) abundance, biomass, secondary production and production to biomass ratios (P : B) of shrimps in Prieta and Bisley. Error bars represent bootstrapped 95% confidence intervals.
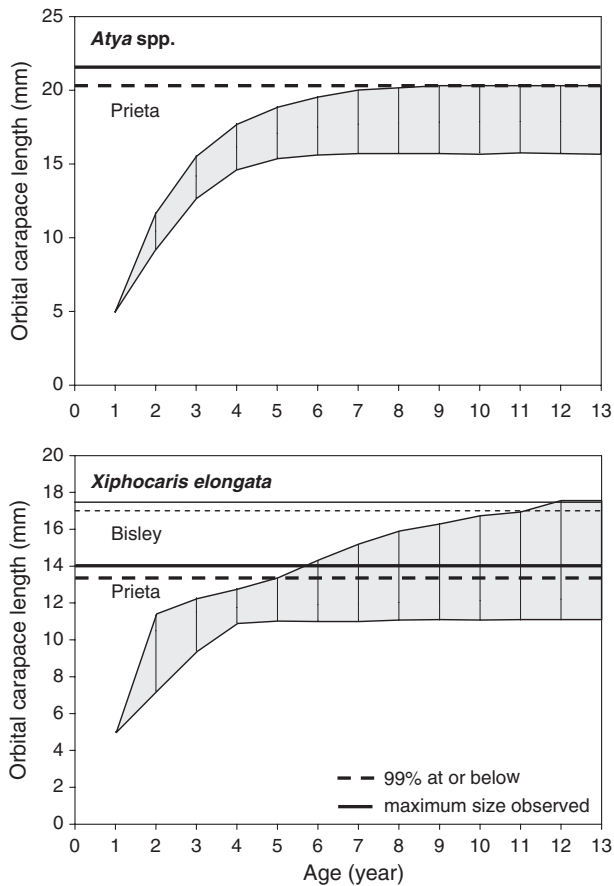
Fig. 4 Results from minimum longevity models of *Atya* spp. and *Xiphocaris elongata*. At each age, the width of the grey envelope represents the bootstrapped 95% confidence intervals of orbital carapace length for 1000 individuals that have grown to that age. The solid line represents the size of the largest individual observed throughout the study. The dashed line represents the size threshold that includes 99% of individuals observed throughout the study.

elevation over relatively short distances result in catchments with high variability in slope, erosive forces, and patterning of knickpoints and associated waterfalls. Headwater streams above large waterfalls lack many predatory fish such as mountain mullet and American eel because these taxa are unable to disperse above large waterfalls (Covich & McDowell, 1996; Covich *et al.*, in press). In these streams, freshwater shrimps escape strong predation pressure, are often very abundant, and exert strong top–down effects on basal resource quantity and quality (e.g. Pringle *et al.*, 1999; March *et al.*, 2002; Cross *et al.*, 2008). We have shown that such differences in fish distributions translate to extreme differences in rates

of secondary production and consumption by shrimps, consistent with cascading indirect effects of landscape topography on biotic processes in streams.

Secondary production is usually estimated at the site or reach scale, with the assumption that major losses or gains to the study area are negligible or at equilibrium. In the case of migratory populations, lifetime production may be spread over a wide range of habitats and environmental conditions, each with a unique set of constraints to production (e.g. Huryn & Gibbs, 1999). For tropical freshwater shrimps, a significant amount of somatic production probably occurs before individuals complete their upstream migration into headwater streams (i.e. in the estuary or during the upstream migration). Whether or not it is important or relevant to quantify this 'external' production will depend on the scale of interest for a given study. Our study was specifically aimed at quantifying production dynamics in headwater streams to place shrimps in an ecosystem context for these high-elevation systems. Questions related to longitudinal patterns of production, or total production at the landscape scale will require a broader study design. Such an approach would require considerable effort but could provide important insights for understanding the ecosystem-level role of migratory species. Surprisingly, few studies have attempted to quantify production at such landscape scales, even for charismatic and commercially important migratory taxa, such as Pacific and Atlantic salmon.

At our study sites, shrimps exhibit a slow-growth, long-lived life-history strategy. Daily growth rates were quite low in comparison to many other stream taxa (Huryn & Wallace, 2000), and the majority of shrimp growth occurred during the first 2–3 years of the larval life span. Our results contrast somewhat with studies of non-migratory tropical shrimps (*Caridina* spp.) in Hong Kong streams, where Yam & Dudgeon (2006) showed that daily growth rates and production of *Caridina* spp. were two to four times higher than shrimps in our study, and demonstrated that life spans of *Caridina* spp. were relatively short (17–22 months). Reasons for these differences are difficult to ascribe to specific mechanisms, but may reflect compensatory adaptation to a higher degree of seasonality with regard to temperature (12–18 °C annual range) and precipitation (distinct wet and dry seasons) in the Hong Kong streams; food quality, phylogeny and average body size may also play
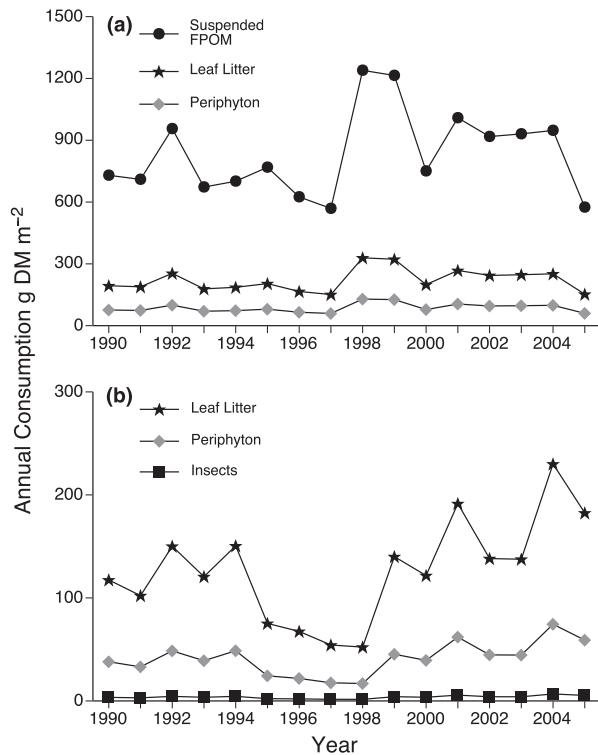
Fig. 5 Annual variation in areal consumption (g DM m^{-2}) of resource categories by (a) *Atya lanipes* and (b) *Xiphocaris elongata* (note different vertical axis scales) in a single pool (pool 0).

population estimates. Depletion sampling, however, requires considerable time and effort, and may not be necessary for detecting variability and/or response of shrimp consumers to environmental perturbations over long time scales (e.g. Covich *et al.*, 1991, 2003).

We estimated minimum life spans between 5 and 11 years for shrimps in our Puerto Rican headwater streams. These life spans appear relatively protracted, but are not outside the range of other slow-growing invertebrates. For example, some freshwater mussels are known to live for over 50 years (Stober, 1972), and crayfish in New Zealand streams may live for >25 years (Whitmore & Huryn, 1999). Our estimates of longevity represent *minimum* life spans because the survival time following somatic growth is yet unknown and observational evidence from Prieta suggests shrimps may actually live considerably longer than our minimum estimates. Individuals marked with elastomer dye in 1991 are still periodically captured in Prieta, and these shrimps were marked at a size corresponding to 1- to 3-years old (T.A. Crowl, S.L. Johnson & A.P. Covich, unpubl. data). Together with our longevity estimates, these recaptures suggest that some individuals in high elevation Puerto Rican streams are capable of living at least 18 years.

For these long-lived shrimps, metabolism is predominantly geared towards maintenance and reproduction. Most shrimps in Puerto Rico are believed to be iteroparous, producing multiple broods per year. Our study did not explicitly examine egg and larval production, but there is reason to believe that larvae represent a significant component of total production by shrimps in tropical headwater streams. In a 4-year

important roles. However, it is important to point out that our estimates of production are conservative because minnow trap sampling did not include very small individuals, which may represent a substantial proportion of biomass and production in some streams (Fig. 2). We recommend pass-depletion sampling over minnow traps for more accurate shrimp

Table 3 Estimated annual consumption of resource categories (g DM m^2) by *Atya lanipes* and *Xiphocaris elongata* during 3 years (2003–05) in the Prieta and Bisley streams based on bioenergetics modelling

	Prieta			Bisley		
Resource category	2003	2004	2005	2003	2004	2005
Atya lanipes						
SFPOM	1049.5 (675.4–1479.9)	440.1 (295.5–593.3)	607.0 (382.8–941.1)	–	–	–
Leaf litter	278.8 (179.4–393.1)	116.9 (78.5–157.6)	161.2 (101.7–250.0)	–	–	–
Periphyton	109.3 (70.4–154.2)	45.8 (30.8–61.8)	63.2 (39.9–98.0)	–	–	–
Xiphocaris elongata						
Leaf litter	172.5 (134.8–210.4)	144.2 (107.4–180.7)	93.4 (51.2–152.9)	3.7 (1.1–7.0)	3.9 (0.9–7.9)	2.8 (0.5–5.9)
Periphyton	55.8 (43.6–68.1)	46.7 (34.7–58.5)	30.2 (16.6–49.5)	1.2 (0.4–2.2)	1.3 (0.3–2.6)	0.9 (0.2–1.9)
Insects	5.1 (4.0–6.2)	4.2 (3.2–5.3)	2.7 (1.5–4.5)	0.1 (0.0–0.2)	0.1 (0.0–0.2)	0.1 (0.0–0.2)

SFPOM, suspended fine particulate organic matter.
Data are means with ranges based on 95% confidence limits from bootstrapping of shrimp density data (see text).

study in Prieta, Johnson *et al.* (1997) found that a high, but variable proportion of shrimps was gravid between April and December; during certain sampling events, gravid females represented up to 50% of the population. If we assume, conservatively, that 25% of the population is gravid for 9 months of the year, we estimate *c.* 4 gravid individuals per m^2. If each individual produces an average of 1200 eggs per brood (T.A. Crowl, unpubl. data), the weight of individual drifting larvae is 0.025 mg (March *et al.*, 1998) and embryonic development time is 25 days (Mashiko, 1990; Yam & Dudgeon, 2005), then production of larvae is estimated to be 4.8 mg DM m^{-2} day^{-1} (Pickard & Benke, 1996). Over an entire year (assuming 9 months of larval production), this represents 1.32 g DM m^{-2} year^{-1} (or *c.* 0.99 g AFDM m^{-2} year^{-1}). Thus, based on these conservative calculations, reproductive output is estimated to be roughly equivalent to somatic production in Prieta. However, nearly all of this production is exported downstream.

Shrimp P : B ratios were low, and conservative estimates of biomass replacement time ranged from 2.5 to 10 years. These slow replacement times suggest that any catastrophic loss in shrimp abundance from natural or anthropogenic causes will be sustained over rather long time scales and that population recovery will be dependent on rates of upstream migration. Indeed, recolonization of shrimp populations from a harvest-related poisoning event at relatively high-elevation within El Yunque took several years (Greathouse, March & Pringle, 2005). However, at lower elevations, recovery from a recent poisoning event occurred within a few months, presumably reflecting the large upstream source of adult colonists (Greathouse *et al.*, 2005). Thus, it is likely that recovery will largely depend on landscape position, with headwater reaches being the most vulnerable to population depletion. Previous studies in Puerto Rico that have examined the response of shrimp populations to natural disturbances (i.e. hurricanes) have generally found rapid recovery or increased abundance (Covich *et al.*, 1991). However, shrimps in Puerto Rico have evolved with such disturbances and probably exhibit adaptive behavioural or reproductive strategies to deal with these events.

Our bioenergetics modelling utilized parameters derived from other species, as well as estimates of some model inputs (e.g. diet proportions). Moreover, we did not include some potentially important met-

abolic costs (i.e. reproduction, moulting), inclusion of which would have increased consumption estimates. Therefore, potential error around the model output must be stressed. However, the modelling of *Atya* spp. and *X. elongata* consumption resulted in values that agree well with independent data based on direct measurements of egestion (i.e. an average total consumption rate of *c.* 0.005 g DM g^{-1} DM h^{-1}; see Cross *et al.*, 2008). These consumption estimates complement the few stable isotope data available from nearby streams in Puerto Rico. Using stable isotope (C and N) analysis, March & Pringle (2003) reported that algae were of overriding importance for trophic support of *Atya* spp. and *X. elongata* populations in the Sonadora stream in Puerto Rico (a catchment adjacent to the Prieta). The Sonadora wetted channel is wider and has less canopy cover than the Prieta (W. F. Cross, pers. obs.), so organic matter inputs from primary production may be higher in the Sonadora. More importantly, stable isotope data provide fundamentally different information from consumption rates estimated from bioenergetic modelling. The former reveal the relative contribution of organic matter sources to consumer assimilation, while the latter estimates rates of organic matter processing by consumers. Consequently, shrimps may be more important processors of terrestrially derived coarse and fine particulate organic matter than is indicated by stable isotope analysis alone (as has been found with crayfishes; Whitledge & Rabeni, 1997). Bioenergetic modelling also has advantages over simpler bioenergetic approaches such as the application of gross growth efficiencies or trophic basis of production. These simpler bioenergetic approaches are based on consumer growth. Growth of large shrimps was not always measurable in our study, even though these individuals have significant energy costs associated with respiration and maintenance. These basal energetic demands would not be incorporated into growth-based consumption estimates (e.g. trophic basis of production), but are integral to the bioenergetic modelling approach used in our study.

The consumption estimates indicated that landscape-scale differences in population densities of these two species leads to large spatial differences in consumption and processing of organic matter resources. However, the proportion of organic matter inputs consumed and processed by shrimps probably varies in significance among resource categories, even

in streams with high shrimp densities. For example, the substantial consumption of SFPOM by *Atya* spp. (the most important resource for that taxon) is probably only a minor proportion of total FPOM fluxes through a stream such as the Prieta (208 kg DM year⁻¹ in a smaller adjacent stream, Quebrada Toronja; McDowell & Asbury, 1994). Combined annual consumption of leaf litter of approximately 350 g DM m⁻² year⁻¹ by the two taxa is likely of moderate significance (i.e. equal to *c.* 40–60% of direct litter inputs; Vogt *et al.*, 1996; Beard *et al.*, 2005). In contrast, consumption of primary production by *Atya* spp. and *X. elongata* may be very significant based on a recent study in Bisley (i.e. approaching 100% for primary producers, Ortiz-Zayas *et al.*, 2005). The proportion of insect secondary production consumed by shrimps is still uncertain, but may be significant in some tropical streams where insect production is low (e.g. Ramírez & Pringle, 1998; Crowl *et al.*, 2000).

In Puerto Rico and many other tropical islands, development and associated increases in water demand have led to widespread construction of dams (Holmquist, Schmidt-Gengenbach & Yoshioka, 1998; Benstead *et al.*, 1999; March *et al.*, 2003). Like large waterfalls, these dams lead to strong discontinuities in the longitudinal distribution of migratory fauna (Holmquist *et al.*, 1998). In extreme cases, in which there is total loss of spillway discharge over a dam, migratory fishes and shrimps are completely absent upstream (Holmquist *et al.*, 1998). These localized extinctions have large effects on the standing stock of organic matter and nutrients, with potentially large effects on ecosystem-scale processes (Greathouse *et al.*, 2006). Our results reinforce the need to recognize the effects that these physical structures exert on shrimp populations and, consequently, on spatial patterns of organic matter distribution and processing across stream catchments (Pringle *et al.*, 1999).

Acknowledgments

References

Bauer R.T. (2004) *Remarkable Shrimps – Adaptations and Natural History of the Carideans.* University of Oklahoma Press, Norman, OK.

Beard K.H., Vogt K.A., Vogt D.J., Scatena F.N., Covich A.P., Sigurdardottir R., Siccama T.C. & Crowl T.A. (2005) The response of structural and functional characteristics of a tropical forested ecosystem to multiple, natural disturbances in legacy environments. *Ecological Monographs*, **75**, 345–361.

Benke A.C. & Huryn A.D. (2006) Secondary productivity of macroinvertebrates. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 691–710. Elsevier, New York, NY.

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

Benstead J.P., March J.G. & Pringle C.M. (2000) Estuarine larval development and upstream post-larval migration of freshwater shrimps in two tropical rivers of Puerto Rico. *Biotropica*, **32**, 545–548.

Blanco J.F. & Scatena F.N. (2006) Hierarchical contribution of river-ocean connectivity, water chemistry, hydraulics, and substrate to the distribution of diadromous snails in Puerto Rican streams. *Journal of the North American Benthological Society*, **25**, 82–98.

Bright G.R. (1982) Secondary benthic production in a tropical island stream. *Limnology and Oceanography*, **27**, 472–480.

Chace F.A. & Hobbs H.H. (1969) The freshwater and terrestrial decapod crustaceans of the West Indies with special references to Dominica. *United States National Museum Bulletin*, **292**, 1–258.

Covich A.P. (1988) Atyid shrimp in the headwaters of the Luquillo Mountains, Puerto Rico: filter feeding in natural and artificial streams. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **23**, 2108–2113.

Covich A.P. & McDowell W.H. (1996) The stream community. In: *The Food Web of a Tropical Rain Forest* (Eds D.P. Reagen & R.B. Waide), pp. 433–459. The University of Chicago Press, Chicago, IL.

Covich A.P., Crowl T.A., Johnson S.L., Varza D. & Certain D.L. (1991) Post-Hurricane Hugo increases in atyid shrimp abundances in a Puerto Rican montane stream. *Biotropica*, **23**, 448–454.

Covich A.P., Crowl T.A. & Scatena F.N. (2003) Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology*, **48**, 1199–1206.

Covich A.P., Crowl T.A., Hein C.L., Townsend M.J. & McDowell W.H. Predator–prey interactions in river networks: a watershed comparison of spatial refugia in freshwater shrimps. *Freshwater Biology* (in press).

Cross W.F., Ramírez A., Santana A. & Santiago L.S. (2008) Toward quantifying the relative importance of invertebrate consumption and bioturbation in Puerto Rican streams. *Biotropica*, **40**, 477–484, doi: 10.1111/j.1744-7429.2007.00388.x.

Crowl T.A., Bouwes N., Townsend M.J., Covich A.P. & Scatena F.N. (2000) Estimating the potential role of freshwater shrimp on an aquatic insect assemblage in a tropical headwater stream: a bioenergetics approach. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **27**, 2403–2407.

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

Crowl T.A., Covich A.P., Scatena F.N., Phillips R., Townsend M.J. & Vinson D.K. (2002) Particulate organic matter dynamics in tropical headwater streams: a comparison of biotic and abiotic factors. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **28**, 923–927.

Crowl T.A., Welsh V., Heartsill-Scalley T. & Covich A.P. (2006) Effects of different types of conditioning on leaf-litter shredding by *Xiphocaris elongata*, a Neotropical freshwater shrimp. *Journal of the North American Benthological Society*, **25**, 196–206.

Cummins K.W. & Wuycheck J.C. (1971) Caloric equivalents for investigations in ecological energetics. *Mitteilungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **18**, 1–158.

Efron B. (1979) Bootstrap methods: another look at the jackknife. *Annals of Statistics*, **7**, 1–26.

Fievet E. (1999) An experimental survey of freshwater shrimp upstream migration in an impounded stream of Guadeloupe Island, Lesser Antilles. *Archiv für Hydrobiologie*, **144**, 339–355.

Franco A.R., Ferreira J.G. & Nobre A.M. (2006) Development of a growth model for penaeid shrimp. *Aquaculture*, **259**, 268–277.

Greathouse E.A. (2005) *Large Dams and Migratory Biota Affect Tropical Stream Ecosystems at Different Scales in Puerto Rico*. Dissertation, Institute of Ecology, University of Georgia, Athens, GA.

Greathouse E.A. & Pringle C.M. (2006) Does the river continuum concept apply on a tropical island? Longitudinal variation in a Puerto Rican stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 134–152.

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

Greathouse E.A., Pringle C.M., McDowell W.H. & Holmquist J.G. (2006) Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico. *Ecological Applications*, **16**, 339–352.

Hanson P.C., Johnson T.B., Schindler D.E. & Kitchell J.F. (1997) *Fish Bioenergetics 3.0*. University of Wisconsin, Sea Grant Institute, Madison, WI.

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

Huryn A.D. & Gibbs K.E. (1999) Macroinvertebrates of riparian sedge meadows in Maine: a community structured by river floodplain interaction. In: *Invertebrates in Freshwater Wetlands of North America: Ecology and Management* (Eds D.P. Batzer, R.B. Rader & S.A. Wissinger), pp. 363–382. Wiley & Sons, New York.

Huryn A.D. & Wallace J.B. (1987) Production and litter processing by crayfish in an Appalachian mountain stream. *Freshwater Biology*, **18**, 277–286.

Huryn A.D. & Wallace J.B. (2000) Life history and production of stream insects. *Annual Review of Entomology*, **45**, 83–110.

Huryn A.D., Koebel J.W. & Benke A.C. (1994) Life history and longevity of the pleurocerid snail *Elimia*: a comparative study of eight populations. *Journal of the North American Benthological Society*, **13**, 540–556.

Iwasa Y. & Miura T. (1976) The rates of respiration and ammonia excretion of freshwater shrimps in Lake Biwa. *Physiology and Ecology (Japan)*, **17**, 465–472.

Jayachandran K.V. (2001) *Palaemonid Prawns: Biodiversity, Taxonomy, Biology and Management*. Science Publishers, Enfield, NH.

Johnson S.L., Covich A.P., Crowl T.A., Estrada-Pinto A., Bithorn J. & Wurtsbaugh W.A. (1997) Do seasonality and disturbance influence reproduction in freshwater atyid shrimp in headwater steams, Puerto Rico? *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **26**, 2076–2081.

Manly B.F.J. (2001) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edn. Chapman and Hall/CRC, New York.

Mantel S.K. & Dudgeon D. (2004a) Dietary variation in a predatory shrimp, *Macrobrachium hainanense* (Palaemonidae), in Hong Kong forest streams. *Archiv für Hydrobiologie*, **160**, 305–328.

Mantel S.K. & Dudgeon D. (2004b) Growth and production of a tropical predatory shrimp, *Macrobrachium hainanense* (Palaemonidae), in two Hong Kong streams. *Freshwater Biology*, **49**, 1320–1336.

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

March J.G., Benstead J.P., Pringle C.M. & Scatena F.N. (1998) Migratory drift of larval freshwater shrimps in two tropical streams, Puerto Rico. *Freshwater Biology*, **40**, 261–273.

March J.G., Benstead J.P., Pringle C.M. & Ruebel M.W. (2001) Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 470–478.

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

March J.G., Benstead J.P., Pringle C.M. & Scatena F.N. (2003) Damming tropical island streams: problems, solutions, and alternatives. *BioScience*, **53**, 1069–1078.

Mashiko K. (1990) Diversified egg and clutch sizes among local populations of the fresh-water prawn *Macrobrachium nipponense*. *Journal of Crustacean Biology*, **10**, 306–314.

McDowell W.H. & Asbury C.E. (1994) Export of carbon, nitrogen, and major ions from three tropical montane watersheds. *Limnology and Oceanography*, **39**, 111–125.

Ortiz-Zayas J.R., Lewis W.M., Saunders J.F., McCutchan J.F. & Scatena F.N. (2005) Metabolism of a tropical rainforest stream. *Journal of the North American Benthological Society*, **24**, 769–783.

Pickard D.P. & Benke A.C. (1996) Production dynamics of *Hyalella azteca* (Amphipoda) among different habitats in a small wetland in the southeastern U.S.A. *Journal of the North American Benthological Society*, **15**, 537–550.

Poff N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391–409.

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**, 125–140.

Pringle C.M. (1997) Exploring how disturbance is transmitted upstream: going against the flow. *Journal of the North American Benthological Society*, **16**, 425–438.

Pringle C.M., Blake G.A., Covich A.P., Buzby K.M. & Finley A. (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., Hemphill N., McDowell W.H., Bednarek A. & March J.G. (1999) Linking species and ecosystems: different biotic assemblages cause interstream differences in organic matter. *Ecology*, **80**, 1860–1872.

Ramírez A. & Hernández-Cruz L.R. (2004) Aquatic insect assemblages in shrimp-dominated tropical streams, Puerto Rico. *Biotropica*, **36**, 259–266.

Ramírez A. & Pringle C.M. (1998) Structure and production of a benthic insect assemblage in a neotropical stream. *Journal of the North American Benthological Society*, **17**, 443–463.

Rudstam L.G. (1989) A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta*. *Journal of Plankton Research*, **11**, 971–983.

Scatena F.N. & Larsen M.C. (1991) Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica*, **23**, 317–323.

de Souza M.L. & Moulton T.P. (2005) The effects of shrimps on benthic material in a Brazilian island stream. *Freshwater Biology*, **50**, 592–602.

Stober Q.J. (1972) Distribution and age of *Margaritifera margaritifera* (L) in a Madison river (Montana, U.S.A.) mussel bed. *Malacologia*, **11**, 343–350.

Townsend M.J., Crowl T.A., Phillips R., Covich A.P. & Scatena F.N. (2002) Indirect and direct abiotic controls on a species-poor stream insect assemblage. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **28**, 919–922.

Vogt K.A., Vogt D.J., Boon P. *et al.* (1996) Litter dynamics along stream riparian and upslope areas following Hurricane Hugo, Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **28**, 458–470.

Whitledge G.W. & Rabeni C.F. (1997) Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotopes and gut analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2555–2563.

Whitmore N. & Huryn A.D. (1999) Life history and production of *Paranephrops zealandicus* in a forest stream, with comments about the sustainable harvest of a freshwater crayfish. *Freshwater Biology*, **42**, 467–478.

Winberg G.G. (1956) *Rate of Metabolism and Food Requirements of Fishes*. Translation Series No. 194, Fisheries Research Board of Canada, Nanaimo, BC.

Yam R.S.W. & Dudgeon D. (2005) Inter- and intraspecific differences in the life history and growth of *Caridina* spp. (Decapoda: Atyidae) in Hong Kong streams. *Freshwater Biology*, **50**, 2114–2128.

Yam R.S.W. & Dudgeon D. (2006) Production dynamics and growth of atyid shrimps (Decapoda: *Caridina* spp.) in 4 Hong Kong streams: the effects of site, season, and species. *Journal of the North American Benthological Society*, **25**, 406–416.

Zippin C. (1958) The removal method of population estimation. *Journal of Wildlife Management*, **22**, 82–90.

Zou X.M., Zucca C.P., Waide R.B. & McDowell W.H. (1995) Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. *Forest Ecology and Management*, **78**, 147–157.