Life history of *Lepidostoma hirtum* in an Iberian stream and its role in organic matter processing

Azevedo-Pereira H.V.S.[1,*], Graça M.A.S.[1] & González J.M.[2]

[1]*IMAR – Instituto do Mar – CIC, Departamento de Zoologia, Universidade de Coimbra, 3004-517 Coimbra, Portugal*
[2]*Departamento Matemáticas y Física Aplicadas y Ciencias de la Naturaleza, Universidad Rey Juan Carlos, C/ Tulipán, s/n, E 28933 Móstoles, Madrid, España*
(*Author for correspondence: E-mail: rike@bio.ua.pt)

Abstract

The goal of this research was to determine the role of *Lepidostoma hirtum* Fabricius 1775 in the fragmentation of allochtonous organic material, in a segment of a mountain river in central Portugal. For this purpose, we measured leaf fragmentation and growth rates at four temperatures (9, 12, 15 and 18 °C) and four leaf types (alder, *Alnus glutinosa* L.; oak, *Quercus andegavensis* Hy; poplar, *Populus × canadensis* Moench; and chestnut, *Castanea sativa* Mill.). Growth rates ranged from 0.012 to 0.049 mg AFDW day^{-1} with no significant effect of temperature and leaf type. Fragmentation/consumption rates were significantly higher for alder (1.62 mg animal^{-1} day^{-1}) than for other leaf types, and significantly lower at 9 °C (0.70 mg animal^{-1} day^{-1}) than at any other temperature (1.12 mg animal^{-1} day^{-1}). In the studied stream, *L. hirtum* larvae had a univoltine life history, with an asynchronous development. Secondary production of *L. hirtum* ranged from 53.95 mg m^{-2} year^{-1} (pools) to 63.12 mg m^{-2} year^{-1} (riffles). Annual P/B ratios differ between habitats: they were 4.01 year^{-1} for pools and 4.49 year^{-1} for riffles. Considering the average density of this species in the study river and their consumption rates, this species has the potential to fragment 8.6 times the mean annual standing stock of organic matter, in the study location.

Introduction

Allochtonous organic material has been referenced as the major energy source for small forest streams (e.g. Fisher & Likens, 1973; Graça, 1993; Abelho, 2001). Riparian vegetation produces high quantities of detritus that enters in headwater streams and is used as an energy source by microorganisms and invertebrates (Abelho, 2000). The quantity and quality of leaf material entering streams depends on the type of riparian vegetation and the properties of the stream, such as its retention capabilities (Friberg & Jacobsen, 1999) and water chemistry, particularly nutrients and hardness (Suberkropp & Chauvet, 1995).

Leaves entering streams also differ in their physical and chemical properties. Those differences influence microbial decomposition (Canhoto & Graça, 1996) and invertebrate feeding and growth (Canhoto & Graça, 1996; Friberg & Jacobsen, 1999; González & Graça, 2003). Invertebrate feeding and growth are also affected by temperature, as it is an important determinant of metabolism (Sutcliffe *et al.*, 1981; Nolen & Pearson, 1993; González & Graça, 2003).

Detritivores feeding on coarse particulate organic matter (i.e., shredders) may account up to 40% of the total invertebrates in low-order streams (Graça et al., 2001a) and they may be limited by food (Gee, 1988; Dobson & Hildrew,

1992). The ingestion rates of shredders are strongly affected by the physico-chemical quality of the leaves and by environmental temperatures (e.g. González & Graça, 2003).

In a previous paper, González & Graça (2003) estimated the amount of leaf litter ingested by the shredding caddis fly *Sericostoma vittatum* Rambur in a small stream in central Portugal. They found that *S. vittatum* had two overlapping cohorts, each needing about one year to develop. Secondary production was 0.44 g m^{-2} year^{-1} and annual leaf litter consumption by this species was estimated as 14–22 g m^{-2}, depending on the diet.

The aim of this study was to determine, in a first stage, the temporal dynamics and to quantify the secondary production of a population of the shredder trichoptera *Lepidostoma hirtum* Fabricius that was sympatric with the *S. vittatum* population studied by González & Graça (2003). In a second stage, we tested in the laboratory the null hypothesis that leaf fragmentation rates of *L. hirtum*, were independent of leaf type and temperature. Data on processing rates and densities allow us to determine the relative importance of this species in leaf litter processing in the studied segment of the headwater stream.

Materials and methods

Population dynamics

This research was carried out in the S. João stream, Lousã Mountains, central Portugal. The study site was located just upstream of the city of Lousã (5th order stream). In this location, the stream is bordered by diverse riparian trees, including chestnut (*Castanea sativa* Mill), pine (*Pinus pinaster* Aiton), eucalyptus (*Eucalyptus globulus* Labill), acacia (*Acacia dealbata* Link), poplar (*Populus × canadensis* Moench) and willow (*Salix* sp.). At the sampling site, riffles and run areas occupied approximately 76% of the stream, in which cobbles and pebbles constituted the substrate. Specimens of *L. hirtum* were collected monthly between November of 2000 and October of 2001. During that period, daily mean water temperatures ranged from 3.9 to 19.9 °C (González & Graça, 2003).

Eleven random samples were taken on each sampling date: seven in riffles, using a Surber sampler (0.09 m^2; 250 μm mesh size) and four in pools, using a Hess sampler (0.025 m^2; 250 μm mesh size). Different sampling devices were used because unlike the Surber, the Hess sampler can be used in the absence of current, which was the case in the pools. Moreover, sampling effort was higher in riffles than in pools due to the high amounts of sediment and fine debris in the pool samples. Samples were transported in a cooler to the laboratory, where the invertebrates were sorted live within 48 h and all coarse particulate organic matter (CPOM) removed. Ash-free dry mass (AFDM) was determined to the nearest 0.1 mg. Specimens of *L. hirtum* were counted and the distance between eyes (E.D.) was measured (precision 20 μm) using a dissecting microscope with an ocular micrometer.

Estimation of individual larval mass was done by a size-mass regression: a group of 46 animals were photographed on a dissection microscope (Wild Heerbrugg® 25×, in which a video camera was inserted – Sony DXC-107AP®), and their E.D. was measured from computer pictures, using Coreldraw9®. The case was removed from each specimen and dry mass (60 °C, 48 h) and ash content (550 °C, 5 h) determined. With these data, we built a regression model to calculate AFDW (mg) from E.D. (mm): $AFDW_{animal} = 0.0409 * e^{3.451 * ED}$, $n = 46$; $R^2 = 0.7031$. Secondary production of *L. hirtum* was estimated using the size-frequency method, as explained in Benke (1984).

Growth

The purpose of this experiment was to investigate how temperature and leaf type affect growth rates of *L. hirtum*. Four standard temperatures were selected: 9, 12, 15 and 18 °C, representing some typical summer and winter temperatures found in the field (González & Graça, 2003). The photoperiod was set to 12:12 h light/dark.

Specimens of *L. hirtum* were collected from the stream from October 2001 to September 2002 and placed in beakers with aerated stream water. They were fed with a mixture of chestnut, oak, poplar and alder leaves during a 1-week acclimation period. The individual mass of each specimen was

calculated from its E.D., using the size–mass regression shown above.

As food, leaves from four tree species were selected: alder, *Alnus glutinosa* L.; oak, *Quercus andegavensis*; poplar, *P. × canadensis* Moench and chestnut, *C. sativa* Mill. Recently shed alder and poplar leaves were gathered from the soil surface in autumn, and senescent oak and chestnut leaves were collected directly from trees. They were air-dried and stored in the dark. Before being offered as food to the animals, leaves were kept in 0.5 mm mesh bags and conditioned for 2 weeks in the stream.

Twenty larval specimens of *L. hirtum* (0.2–0.4 mg AFDW) were reared at each temperature and diet. They were individually allocated into beakers with filtered stream water, which were aerated by plastic pipette tips connected to an air pump. Water and food were renewed weekly, and animals measured again after 4 weeks. Growth was given by the difference in mass (log AFDW), divided by time in days.

Fragmentation

The goal of this experiment was to determine how temperature and leaf type affect leaf fragmentation rates, assumed to be proportional to feeding rates. The term fragmentation is here applied, because *L. hirtum* use leaves as food but also as building material for the case, making food consumption difficult to measure directly. Specimens with an initial mass distribution of 0.8–1.5 mg AFDW were reared in beakers at the same temperature and leaf types as described above. A known amount of leaves was provided in the form of leaf discs. Pairs of 9 mm-diameter discs were obtained with a cork borer from contiguous areas of a same leaf, assuming that the two discs from the same pair had identical mass.

We reared specimens of *L. hirtum* individually in beakers containing two pairs of leaf discs. One disc from each pair (exposed) was accessible to *L. hirtum*, while the other one (control) was enclosured in a fine mesh (0.5 mm) envelope, next to the surface of the water.

After 72 h, discs were removed, dried at 60 °C for at least 48 h, weighed, burned at 550 °C for 5 h and reweighed, to determine AFDW. Fragmentation was computed as the difference between control and exposed discs (mg), divided by time (days).

Statistical analysis

Differences between habitats (riffles and pools) and sampling dates for density and standing stocks of CPOM in benthos were tested using two-way ANOVA, followed by a Tukey test (Zar, 1996). The effect of temperature and leaf type on growth and fragmentation were also tested using two-way ANOVA followed by Tukey test when appropriate.

Results

Growth and fragmentation experiments

Mean growth rates of *Lepidostoma hirtum* ranged from 0.012 to 0.049 day^{-1} for chestnut at 15 °C and poplar at 15 °C, respectively. There were no significant differences (two-way ANOVA; $n = 145$; $p > 0.05$) between the leaf types given as food to the animals and nor among the temperatures to which they were subjected (Fig. 1).

Leaf fragmentation rates ranged from 0.41 to 1.81 mg AFDW leaf animal^{-1} day^{-1} for oak at 9 °C and alder at 12 °C, respectively. Unlike growth, fragmentation rates were affected by both temperature and leaf type (two-way ANOVA; $p < 0.05$ in both cases, Table 1, Fig. 2). They were significantly lower at 9 °C than at any other temperature and significantly different among all leaves, with higher fragmentation rates occurring with alder, followed by chestnut, poplar and oak (Table 1, Fig. 2).

Population dynamics

The stock of benthic organic matter ranged from 0.8 mg AFDW (January, pools) to 81.0 mg AFDW in September in pools (González & Graça, 2003). Densities of *L. hirtum* were significantly correlated with the organic matter content in riffles (Spearman Rank Correlation, $p < 0.05$; Fig. 3).

Density of *L. hirtum* at S. João stream ranged from 11 ind. m^{-2} (December, riffles) to 1389 ind. m^{-2} (September, riffles; Fig. 3). In a yearly basis, there were no significant differences between riffles and pools (ANOVA; $n = 110$;
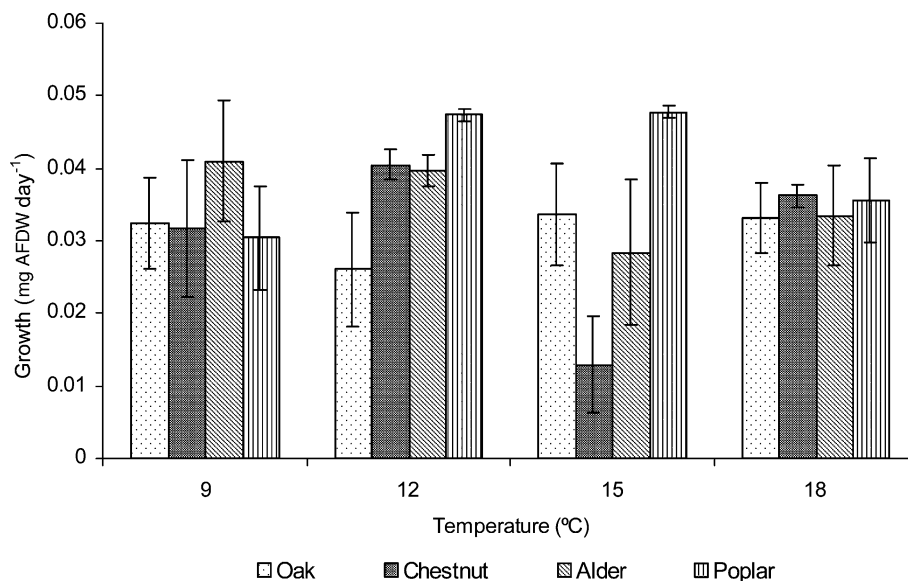
Figure 1. Growth rates of *Lepidostoma hirtum* in terms of daily increase in size for four leaf types and temperatures (mean and standard error).

$p > 0.05$). In October the densities of *L. hirtum* were significantly higher than in December, February, March, April and May (Tukey test, $p < 0.05$).

Lepidostoma hirtum larvae appear to have only one cohort in this year (Fig. 4) with recruitment from May to November. This large recruitment period results in a great asynchrony, due to the coexistence of larvae of different sizes, during practically the entire year, especially between July and October.

For production calculations, a Cohort Production Interval (Benke, 1979) of 12 months (the maximum value for univoltine populations) was used. Overall secondary production of *L. hirtum* in S. João stream was 60.92 mg m^{-2} year^{-1}, with a production of 53.95 mg m^{-2} year^{-1} in pools and 63.12 mg m^{-2} year^{-1} in riffles. The overall annual Production/

Table 1. Two-Way ANOVA and Tukey test for fragmentation rates of *L.* hirtum with four leaf types at four temperatures

Source	Values of F	Values of p	Tukey Test
Temperature (°C)	13.997	<0.05	(18 = 15 = 12) > 9
Leaf type	59.258	<0.05	Ag > Cs > Pc > Qa
Temperature × Leaf type	1.218	0.280	

Ag = *Alnus glutinosa*; Pc = *Populus × canadensis*; Cs = *Castanea sativa*.

Biomass (P/B) ratio was 4.4 year^{-1}, with a ratio of 4.01 year^{-1} in pools and 4.49 year^{-1} in riffles.

Discussion

Fragmentation

The maximum leaf fragmentation rate by *L. hirtum* was 1.61 mg leaf animal^{-1} day^{-1}, for individuals fed on alder leaves. Those values are comparable to the reported feeding rates of other shredders fed similar leaves and temperatures (Table 2). Oak was the least fragmented leaf type, which is comparable to some earlier studies. The low feeding/fragmentation rate is probably due to leaf physical-chemical characteristics, such as low nitrogen content (Irons et al., 1988) and high toughness (Oliveira, 2003). Fragmentation rates are an indicator of consumption rates, and the sequence obtained in this paper is consistent with other similar works, with this shredder using alder in preference to tougher leaves (Iversen, 1974; Irons et al., 1988; Friberg & Jacobsen, 1994, 1999; Jacobsen & Friberg, 1995; González & Graça, 2003).

Therefore, processing rates of leaves (feeding plus material incorporated in the cases) by *L. hirtum* are similar to feeding rates reported for other shredders.
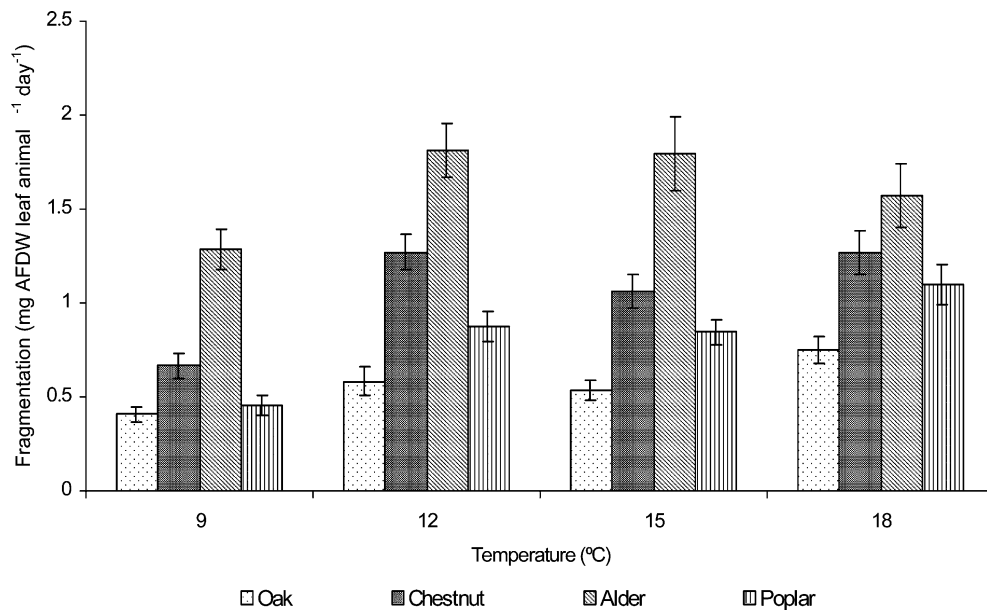
Figure 2. Fragmentation rates of leaves caused by feeding activities of *Lepidostoma hirtum* fed on four leaf types and 4 temperatures (Mean and standard error).

The sequence alder > chestnut > poplar > oak is similar to findings of González & Graça (2003) for the coexisting *Sericostoma vittatum*, but in that case poplar and chestnut were in reverse order.

The high value of alder leaves as a food resource is widely noted in the literature for other shredders (e.g. Iversen, 1974; Jacobsen & Friberg, 1995; Haapala et al., 2001).
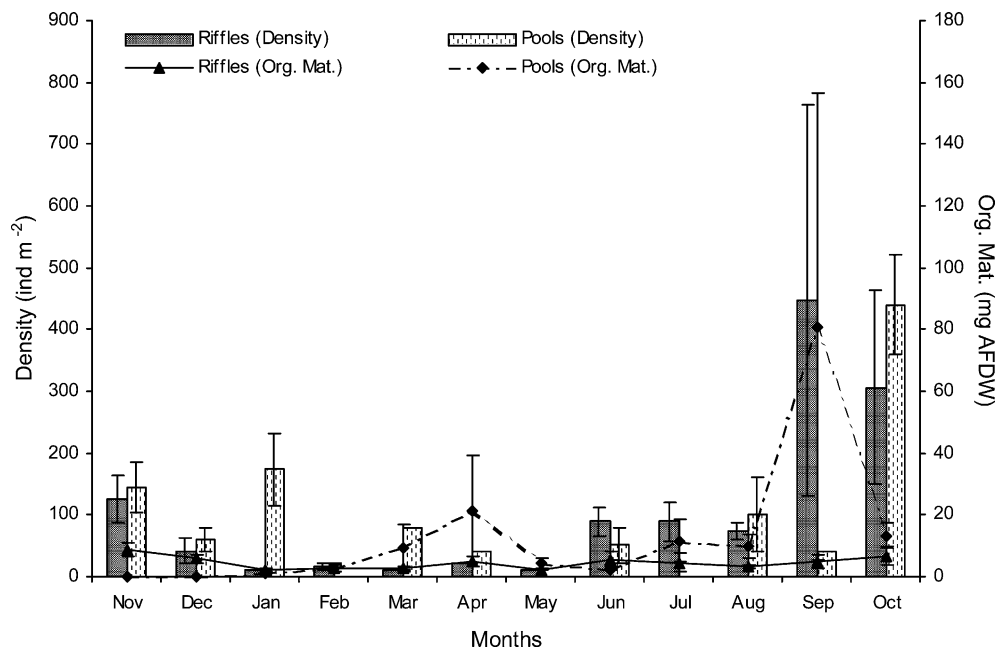

Figure 3. Temporal dynamics of *L. hirtum* densities, and total organic matter in riffles and pools of the S. João stream. Vertical bars represent standard error.
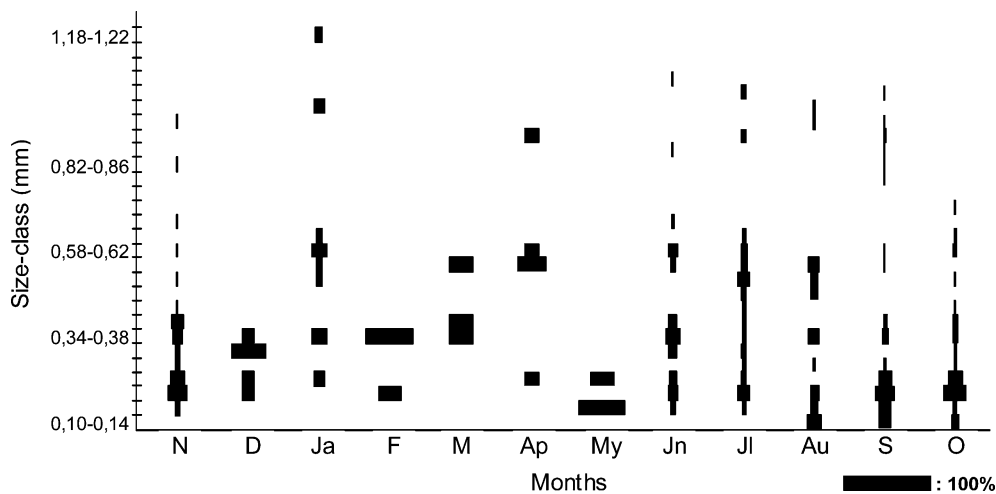
Figure 4. Size-frequency of *Lepidostoma hirtum* larvae from November 2000 to October 2001 in the S. João stream. The width of bars represents the percentage of larvae in each size-class, on a given sampling date.

Knowing that fragmentation rates were significantly lower at 9 °C than at any other tested temperature, and given that metabolism increases with temperature, fragmentation would be expected to increase in the same way. This relation was indeed described by Iversen (1979) for *Sericostoma personatum* (Spence) larvae (high ingestion rate at 13 °C, increasing and decreasing above and below this value); by González & Graça (2003) for *S. vittatum* larvae (maximum consumption rates between 15 and 18 °C); and Grafius & Anderson (1980) for *Lepidostoma unicolor* (Banks). The lack of differences in the range above 9 °C may be related with the high variability in fragmentation rates, which include feeding and use of leaves for case building.

Growth

We also did not find any measurable effect of temperature or leaf type on growth rates. In terms of temperature, we expected an increase in growth with temperature up to a plateau, as reported for other aquatic invertebrates such as *Gammarus pulex* (L.) (e.g. Sutcliffe et al., 1981). According to Iversen (1979), at temperatures higher than 13 °C the increase in consumption by *S. personatum* does not compensate for the increase in metabolic costs, causing a decrease in growth. In terms of food types, in general, consumers grow at high rates when high quality food is offered (e.g. Herbst,

1982; Friberg & Jacobsen, 1994; González & Graça, 2003). Still, some invertebrates increase their consumption rates when fed on low quality food, promoting, in this way, a constant growth rate (e.g. Anderson & Cummins, 1979; Friberg & Jacobsen, 1999). This food plasticity appears to be an advantage in environments where food resources vary seasonally or unpredictably, allowing consumers to move between a range of food resources of variable quality, without compromising significantly their growth performance (Graça et al., 2001b).

Our fragmentation rate experiment did not show this pattern of compensation feeding to allow constant growth. We conclude that a high individual variability in growth may have masked the factors leaf type and temperature in growth. Alternatively, this species may be very tolerant to temperature and food types, which is consistent with its wide distribution (Cummins, 1973; Moretti, 1983; Silveira & Terra, 1994; and Vieira Lanero, 2000) and wide trophic niche (Basaguren et al., 2002).

Population dynamics

Larvae of *Lepidostoma hirtum* in the S. João stream had a univoltine life history, with one long recruitment period. The presence of final stage larvae during almost all the year, for this and for similar species, suggests a temporally extensive

Table 2. Comparison of consumption results of this and other studies

Test species	Consumption/Fragmentation (mg leaf animal⁻¹ day⁻¹)	t °C	Initial animal mass (mg)	Food type	References
Sericostoma personatum	1.6	15	5.7 DM	Alder (*A. glutinosa*)	Friberg & Jacobsen (1994)
Sericostoma personatum	1.1	10	–	Alder (*A. glutinosa*)	Wagner (1990)
Lepidostoma hirtum	1.61	9–18	0.8–1.5 AFDW	Alder (*A. glutinosa*)	Present study
Pycnopsyche luculenta	0.42	15	14.8 DM	Chestnut (*C. dentata*)	Smock & MacGregor (1988)
Sericostoma vittatum	0.47	15	0.81–1.89 DM	Chestnut (*C. sativa*)	Feio & Graça (2000)
Lepidostoma hirtum	1.07	9–18	0.8–1.5 AFDW	Chestnut (*C. sativa*)	Present study
Gammarus pseudolimnaeus	2.09	10	–	Poplar (*P. deltoides*)	Herbst (1982)
Lepidostoma hirtum	0.82	9–18	0.8–1.5 AFDW	Poplar (*P. × canadensis*)	Present study
Pycnopsyche luculenta	0.22	15	14.8 DM	Oak (*Q. rubra*)	Smock & MacGregor (1988)
Lepidostoma hirtum	0.57	9–18	0.8–1.5 AFDW	Oak (*Q. andegavensis*)	Present study

DM = dry mass; AFDM = ash free dry mass.

emergence period (Wallace et al., 1990; González, 2000). Basaguren et al. (2002) found the same pattern for this same species in a Basque Country (Spain) stream. The sympatric *Sericostoma vittatum* also has a univoltine life history (González & Graça, 2003).

Anderson & Cummins (1979) observed high growth rates of shredders during late autumn and winter, at the peak of leaf fall, and suggested that shredder life histories are synchronized to benefit from this pulse of high quality resources. However, despite high densities in late autumn and winter, the life history of *L. hirtum* does not seem to be tied to autumn output of leaves. Winterbourn et al. (1981) suggested that asynchronous (i.e. several size classes present at a given time) development could be viewed as a "bet-hedging" strategy in unpredictable environments. This seems to be the case of *L. hirtum* in S. João stream and is also observed for the other sympatric shredder *S. vittatum* (González & Graça, 2003). Although we could expect a favourable environment for shredders in autumn because of the high litter input, this is also the season of high rains, with occasional floods washing away leaves and other plant detritus.

Densities of this species were similar in riffles and pools, but production was higher in riffles than in pools. This is consistent with other observations (Wohl et al., 1995; González & Graça, 2003). We do not know the reason for the difference, but it could be related to additional food resources in riffles, or to higher accumulations of leaf detritus in riffles than in pools. González & Graça (2003) found no correlation between *S. vittatum* abundance and CPOM stocks. Nonetheless, for the same period and the same river (present study), numbers of *L. hirtum* larvae and organic content were correlated in riffles (Spearman Rank Correlation, $p < 0.05$). We do not know whether *L. hirtum* passively appears where organic matter accumulates, or if this species actively searches for patches with accumulated organic matter.

The secondary production (60.92 mg m^{-2} year^{-1}) found in the S. João stream was very similar to that reported for *L. hirtum* (69 mg m^{-2} year^{-1}) in a Northern Spanish stream (González, 2000), but less than values reported for other *Lepidostoma* species in North American streams (117 mg m^{-2} year^{-1}; Lugthart & Wallace, 1992; and 126 mg m^{-2} year^{-1}; Wohl et al., 1995), and lower than the production reported for the sympatric *S. vittatum* (441 mg m^{-2} year^{-1}; González & Graça, 2003).

Nevertheless, the P/B ratios for both species were comparable: 4.4 year^{-1} for *L. hirtum* and 4.9–5 year^{-1} for the sympatric *S. vittatum*, similar to the ratio reported for *Lepidostoma bryanti* (Banks) on a North American stream 4.5 year^{-1} (Krueger & Waters, 1983) and within the range for other species: 6 year^{-1} for *Lepidostoma* sp. (Lugthart & Wallace, 1992).

Leaf fragmentation in the stream

The annual standing stock of CPOM for the study period was 6.3 g m^{-2}, and the major organic matter input in the stream was composed of leaves of *Acacia dealbata*, *Castanea sativa* and *Salix* spp (González & Graça, 2003). This value is much lower than that reported by Abelho & Graça (1998) for other streams located in central Portugal (157 g m^{-2}). The difference may be related to stream order. While Abelho and Graça (1998) worked in a 1st order stream, our study was carried out in a 4th–5th order reach. It is known that retention (and therefore standing stock of organic matter) decreases with increase in stream order (e.g. Abelho, 2001). For the period between November 2000 and October 2001, annual mean density of *Lepidostoma hirtum* larvae for the study site was 138 individuals m^{-2}, with a maximum of 366 individuals m^{-2} in September 2001. Given that chestnuts are very abundant in the study area, we can assume that these leaves make the highest contribution to the stream. Knowing that these leaves were fragmented at an average rate of 1.07 mg leaf day^{-1}, we can take this value as a mean fragmentation rate for larvae of *L. hirtum* in this stream. We can calculate that, in the field, these animals can fragment around 138*1.07 = 147.7 mg leaf m^{-2} day^{-1}, corresponding to 54 g m^{-2} per year. This value is again rather close to the one calculated by Iversen (1980) for larvae of *S. personatum* on a forest stream where the major arboreal species was beech (50 g m^{-2} year^{-1}), but higher than that reported for the sympatric *S. vittatum* (14–21 g m^{-2} year^{-1}, González & Graça, 2003).

These fragmentation values represent around 8.6 times the annual mean standing stock of CPOM in the S. João stream. Probably this value is unrealistically high, since *L. hirtum* also feeds on other resources (Basaguren et al., 2002). Nevertheless, our results demonstrate that shredder invertebrates in streams have the capability to process large amounts of leaf litter. The fate of detritus in streams is very dynamic; it is quickly used by fungi and eaten by invertebrates at a very high rate. A continuous supply of leaf litter and feeding on alternative sources can explain the high productivity of invertebrates in low-order streams draining forested areas.

Acknowledgements

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