Conversion of leaf litter to secondary production by a shredding caddis-fly

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SUMMARY

1. The aim of this study was to estimate the amount of leaf litter ingested by the shredder caddis-fly *Sericostoma vittatum* in a small stream in central Portugal. The study combined field data on population dynamics and laboratory experiments to determine the effect of temperature (9, 12, 15 and 18 °C), leaf species (*Alnus glutinosa*, *Castanea sativa*, *Populus × canadensis* and *Quercus andegavensis*) and animal mass on growth and consumption rates of the larvae.

2. *Sericostoma vittatum* had two overlapping cohorts, each of which needed about 1 year to complete development. Mean annual density and biomass were 115 individuals m^{-2} and 83 mg m^{-2}, respectively. Secondary production was 0.44 g m^{-2} $year^{-1}$ and production/biomass ratio was 4.9–5 $year^{-1}$.

3. Consumption rates of larvae increased with temperature up to the optimal temperature for growth which varied between 13.7 and 16.7 °C depending on the diet.

4. Consumption rate was positively related to larval mass but growth rate was negatively related with larval mass. Larvae fed on *A. glutinosa* and *P. × canadensis* had higher consumption and growth rates than those fed on *C. sativa* or *Q. andegavensis*.

5. Annual leaf litter consumption by *S. vittatum* was estimated as 14–22 g m^{-2} depending on the diet. No relationship was observed between the amount of detritus consumed by the population of this caddis-fly in the field and either water temperature, the stock of detritus on the stream bottom, or larval abundance. Instead, the temporal dynamics of leaf litter consumption by *S. vittatum* were controlled by its life history.

6. This study highlights the influence of factors such as animal size and water temperature on the invertebrate energetics. Models explaining how these variables affect invertebrate production efficiency may be very important for obtaining accurate estimates of the role of shredders in the energy flow across stream ecosystems.

Keywords: detritus consumption, life history, secondary production, shredder, stream benthos

Introduction

Leaf litter constitutes a major energy source for invertebrate communities dwelling in forested headwater streams (e.g. Fisher & Likens, 1973; Wallace *et al.*, 1997). This material is consumed by animals (detritivores) and microorganisms, which make it available to other organisms in detrital food webs. The relative importance of detritivores and microorganisms in leaf litter breakdown influences rates and pathways of energy flow in these systems (Cummins *et al.*, 1973; Wallace *et al.*, 1991). Moreover, the feeding activities of detritivores in headwaters influence communities in higher order reaches because leaf litter processing generates fine particulate organic matter and dissolved organic matter that are exported further downstream (Vannote *et al.*, 1980; Wallace & Webster, 1996).

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Laboratory experiments have shown that feeding rates of detritivores are influenced by an array of factors including leaf species (e.g. Canhoto & Graça, 1995; Friberg & Jacobsen, 1999), water temperature (e.g. Nolen & Pearson, 1993; Buzby & Perry, 2000) and invertebrate mass (e.g. Iversen, 1979; Feio & Graça, 2000). Nevertheless, such experiments generally fail to quantify the amount of leaf litter consumed by natural populations in the field. Other studies have estimated this amount by excluding fauna from leaf litter breakdown (e.g. Cuffney *et al.*, 1990; Graça *et al.*, 2001), but they only quantify the leaf litter processed by the whole community and do not provide information about the role played by individual populations. Thus, although these analyses give valuable insights, they do not allow us to link population traits (e.g. life history, abundance or production dynamics, feeding preferences) with the general process of leaf litter breakdown. Finally, other researchers have attempted to quantify the amount of food consumed by detritivore populations using data on biomass or secondary production in the field and feeding rates or production efficiency data in the laboratory (e.g. Oertli, 1993; Hieber & Gessner, 2002). In these cases, direct measures of biomass and secondary production are used, but the values of ingestion rates and production efficiency are gathered from the literature, yielding rough estimates of the leaf litter actually consumed.

In this paper we have estimated the amount of leaf litter consumed by a detritivore caddis-fly, *Sericostoma vittatum* Rambur, in a small stream in central Portugal. First, we quantified its secondary production in the field. Then, we measured growth and consumption rates of *S. vittatum* larvae in the laboratory. To obtain accurate estimates of production efficiency by this detritivore, we performed experiments at a broad range of water temperatures using animals of different sizes. The invertebrates were fed with pure diets of each of four leaf species covering a range of fast to slow processing categories (sensu Petersen & Cummins, 1974). This analysis allowed us to quantify both the participation of *S. vittatum* in leaf breakdown in the stream and to explore the links between leaf litter processing and the life history and population dynamics of this caddis-fly.

Methods

Study site

The study site is located in a fourth-order reach of the São Jõao (S. Jõao) stream (40°6′N, 8°14′W) at 230 m above sea level. It drains a small siliceous catchment (18 km²) in the Lousã Mountains (central Portugal). The zone is covered by *Pinus pinaster* Aiton and *Eucalyptus globulus* Labill. plantations, *Acacia dealbata* Link and shrubland stands, and small deciduous woodlands where *Castanea sativa* Mill. is the main species. Forestry is the only human activity upstream of the study site. The stream banks are sparsely covered by *Populus × canadensis* Moench, *Salix* spp., *C. sativa* and *A. dealbata*. Riffle and run areas account for 76% of the stream bottom at the study site and are constituted mainly of cobbles and pebbles, but sand is common in pools. During the period of our study, daily mean water temperature ranged from 3.6 to 19.9 °C (Fig. 1), corresponding to accumulated 4524 degree days. Water conductivity and pH of the water are low at the site (mean annual values were 6.6 and 50 μs cm⁻¹). More information on the study site can be obtained in Graça *et al.* (2001) and Bärlocher & Graça (2002).
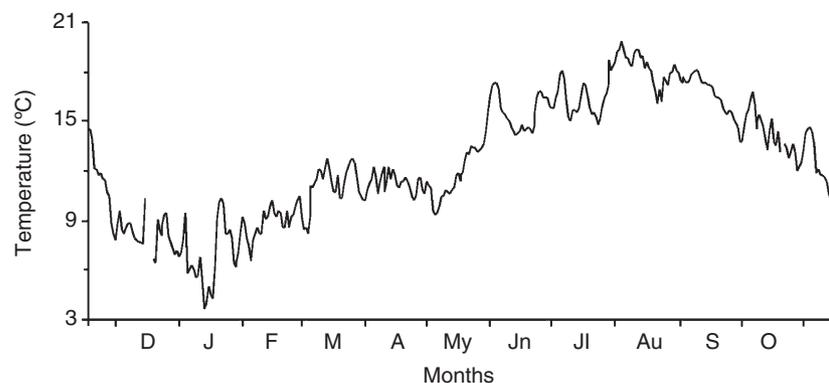

Fig. 1 Daily mean water temperature from November 2000 to November 2001.

Field sampling

Samples of benthos were collected monthly, from November 2000 to November 2001. On each sampling date, seven random samples were taken in riffles using a Surber sampler (0.09 m^2 area, 250 μm mesh) and four random samples were taken in pools with a Hess sampler (0.025 m^2 area, 250 μm mesh). The latter method enabled us to sample only pools with sandy bottoms. The samples were placed in plastic bags, and transported in a cooling box to the laboratory. Within 48 h after collection, they were washed through a series of nested sieves (mesh sizes 20, 1, 0.5 and 0.25 mm). All invertebrates and coarse particulate organic matter (CPOM) retained on the 20 and 1 mm sieves were removed. Invertebrates were preserved in 70% alcohol. CPOM was stored at −20 °C prior to ash-free dry mass (AFDM) determination to ±0.1 mg (see below). Material retained on the other sieves was preserved in 70% alcohol, sorted under 10× magnification and identified. Because no *S. vittatum* larvae were found on the 0.25 mm sieves in the first 35 samples sorted, all 0.25 mm sieve fractions were discarded.

All *S. vittatum* found in the samples were counted and their head widths were measured (precision 20 μm) using an ocular micrometer in a dissecting microscope. Individual larval mass was estimated from a size-mass regression that was constructed with *S. vittatum* larvae taken from the Cerdeira stream, a small nearby tributary of the S. João. These animals were photographed alive with a digital video camera Sony DXC-107AP attached to a dissecting microscope, placed individually beside their cases in preweighed aluminium foils, dried (48 h at 60 °C), weighed (precision 0.01 mg), ashed (6 h at 500 °C) and reweighed to obtain AFDM. The AFDMs of their cases were measured by the same procedure. Head widths of larvae were determined (precision 0.5 μm) by analysing digital images with Corel Draw 9.0 software.

The size frequencies of *S. vittatum* larvae, found on each month, were analysed using Anamod 1.6 software. This program allows various cohorts present in a population to be differentiated assuming that their size distributions follow those of the normal curves (Nogueira, 1992).

Secondary production of *S. vittatum* was estimated using the size-frequency method (SFM) and the instantaneous growth method (IGM) as explained in Benke (1984). For the latter procedure, we followed González *et al.* (2000): negative growth rates found during the recruitment period were recorded as 0, and negative growth rates that occurred during the pupation period were recalculated using daily growth rates found in the previous time interval.

Head width–body mass relationships of *S. vittatum* were fitted to linear, exponential and power models to determine which had strongest correlation (e.g. Smock, 1980; González *et al.*, 2002). Outliers were identified after computing their leverage coefficients and standardised residuals and removed (Sokal & Rohlf, 1995). Density, mean individual mass and population biomass of larvae, and mass of standing stocks of CPOM in benthos were log-transformed before analysis to improve homoscedasticity of data (Sokal & Rohlf, 1995; Zar, 1996). Differences between habitats (riffles versus pools) and sampling dates for the above parameters were tested using two-way anovas, followed by Tukey Honestly Significant Difference Test (Tukey test) for *post hoc* comparisons (Zar, 1996).

Laboratory experiments

Growth and consumption trials were conducted with *S. vittatum* larvae collected from Cerdeira stream. Four water temperatures (9, 12, 15 and 18 °C) and four leaf species: *Alnus glutinosa* (L.) Gaertner (alder), *C. sativa* (chestnut), *P. × canadensis* (poplar) and *Quercus andegavensis* (oak) were used in the trials. Alder and poplar (processing rates 0.012–0.029 day^{-1} and 0.037 day^{-1}, respectively; see references in Abelho, 2001) are fast-breakdown species (Petersen & Cummins, 1974) and chestnut is a medium-breakdown species (processing rate from 0.005 to 0.008 day^{-1}; see Abelho, 2001). We could find no reports of leaf decomposition of *Q. andegavensis* in the literature, but the two parental species of this hybrid (*Q. robur* L. and *Q. pyrenaica* Willd) are slow-breakdown species (0.004–0.005 and 0.003, respectively; see Abelho, 2001).

Senescent leaves of alder, chestnut and poplar were collected in autumn 2000, air-dried and stored at ambient temperature until needed. Only intact leaves were used in experiments. Leaf litter was conditioned in 0.5 mm mesh bags in the Cerdeira stream for 2 weeks prior to the start of each trial.

All experiments were carried out in the laboratory at constant temperature and under a 12 : 12 light/

dark period. Larvae were placed individually in 50 mm diameter glasses with water from the Cerdeira stream, aeration, fine sand that had been sterilised in a muffle furnace (500 °C) and leaf litter. The initial individual mass of larvae used in the experiments ranged from 0.1 to 10.6 mg.

For each growth trial (temperature × leaf species) 20 replicates were included. Trials ran for 28–49 days, depending on the time all the larvae needed to show more than 5% size increment. Growth rate (g, day^{-1}) was assumed to be exponential, and was measured as the difference between final mass (M_f, mg) and initial mass (M_i, mg) divided by the elapsed time (t, days) accordingly to the formula:

$$g = \frac{\ln(M_f) - \ln(M_i)}{t}.$$

The initial and final masses of the larvae were estimated using the head widths measured from photographs taken at the start and at the end of the experiments, and the head width–AFDM relationship (see above).

For each leaf species and temperature we conducted three to five series of consumption experiments with 20 larvae in each series. The invertebrates were photographed before each trial, their head widths were measured and their mass was estimated from the size-mass regression. Pairs of leaf discs were cut with a 9 mm core borer from symmetrical regions of the same leaf and were assumed to have identical mass (e.g. Nolen & Pearson, 1993; Graça *et al.*, 2001). Two discs from separate leaves were given to each animal and the other disc of each pair was submerged in a mesh bag a few centimetres above the glass bottom where they were unavailable to the larvae. After 2 or 3 days, the remains of exposed and control discs were collected and weighed (AFDM). Daily consumption was estimated as the difference in mass between control and exposed leaf discs (mg) divided by the elapsed time in days.

Linear, exponential and power models were fitted to animal mass, daily consumption and growth rate data obtained for each temperature and leaf species; outliers were excluded as described above. Models with the highest correlation coefficients were selected to describe the observed relationships. Comparisons were made among daily consumption or growth rates of (1) animals fed the same leaf species at different temperatures and (2) animals reared at the same temperature but fed different leaf species. For these comparisons, differences among the slopes of the regression lines were tested first; when the differences were not significant, differences among the intercepts were also tested (Sokal & Rohlf, 1995; Zar, 1996). Tukey tests among slopes or intercepts were used for *post hoc* comparisons (Zar, 1996). Finally, multiple regression models were constructed to predict consumption or growth rate from animal mass and water temperature.

Calculation of consumption with field data

Consumption in the field between consecutive sampling dates was estimated using the formula:

$$C = P\ \text{GPE},$$

where P is production during the interval (mg m^{-2} year^{-1}) and GPE is gross production efficiency (mg mg^{-1}).

Gross production efficiencies were calculated as daily production divided by daily consumption. Thus, the formula used was:

$$\text{GPE} = \frac{Mg}{C},$$

where C is daily consumption of leaf litter.

The daily consumption of leaf litter and the growth rate of larvae were calculated from equations describing results obtained in the laboratory experiments. They were specific for each leaf species, and incorporated animal mass and water temperature. The GPE used for a given month was calculated as the arithmetic mean of the GPEs of the animals present at the beginning and end of that month, corrected for daily consumption of leaf litter.

Results

CPOM stocks

The annual mean values of CPOM standing stocks were 3.6 g m^{-2} in riffles and 14.8 g m^{-2} in pools, giving an annual average for the whole stream benthos of 6.3 g m^{-2}. Most CPOM consisted of unidentified fragments of leaf litter, and *A. dealbata*, *C. sativa* and *Salix* spp. leaves. CPOM stocks did not differ between habitats (riffles versus pools) or sampling dates ($P > 0.05$, two-way ANOVA). Nevertheless,

interaction between the factors indicated inter-habitat differences on some dates ($P < 0.05$).

Size-mass regression

The head width–mass relationship for *S. vittatum* was expressed by the following power equation:

$$M = 0.734 \, HW^{3.5211} \quad r^2 = 0.90, \quad n = 61, \quad P < 0.0001,$$

where M is the AFDM of the animal plus its case (mg) and HW is the head width of the animal (mm).

The percentage of total biomass allocated to cases was not correlated with the animal size or mass ($P > 0.05$ in both cases) and averaged 26.4%.

Population dynamics

Sericostoma vittatum had two cohorts in the study year (Fig. 2). Larvae belonging to the first cohort appeared in December, grew during winter and spring, reached maximum size in summer, and pupated in November and December. The recruitment period of the second cohort was June to September. These animals also started growing immediately, attained maximum size in late winter and pupated between April and June. The cohort production intervals (i.e. the mean length of the larval stage; Benke, 1979) of the first and the second cohorts were 11 and 10 months, respectively.

Density and biomass of *S. vittatum* were five and 10 times greater in pools than riffles ($P < 0.0001$, ANOVA), respectively. They were not correlated with CPOM stocks in the sampling units or the sampling dates ($P > 0.05$ in all cases). Highest densities in riffles were observed from August to November and densities were lowest from January to March (Fig. 3a). Very high densities of *S. vittatum* were found in pools in November 2000, but they significantly differed only from densities in February (Fig. 3a). Biomass of *S. vittatum* in riffles did not follow a clear temporal trend, whereas in pools, lowest values were found in February and between July and November (Fig. 3b). However, differences in biomass were not significant ($P > 0.05$, ANOVA).

Mean individual mass was analysed separately for each cohort. No differences in mean mass were found between habitats ($P > 0.05$, ANOVA), whereas the interaction term between habitat and time was significant for the second cohort ($P < 0.0001$), indicating that some differences between riffles and pools could occur on some dates. Irrespective of the habitat sampled, the highest and the lowest mean mass values were observed at the start of each cohort's pupation and recruitment period, respectively.

As the two overlapping cohorts had different cohort production intervals, production was calculated separately for each one. Secondary production of *S. vittatum* was much higher in pools (1429 and 1437 mg m^{-2} year^{-1} using the IGM and the SFM, respectively) than in riffles (134 and 136 mg m^{-2} year^{-1} using the IGM and the SFM, respectively). However, annual production/biomass (P/B) ratios did not differ between habitats: they were 5.0 year^{-1} in riffles and 4.9 year^{-1} in pools when calculated by the SFM, and 4.9 year^{-1} in both habitats when calculated by the IGM. Production estimates for this species in the S. João stream were 441 mg m^{-2} year^{-1} when estimated by the IGM and 444 mg m^{-2} year^{-1} when estimated using the SFM. As no animals were found in pools in February, a daily growth rate was calculated for the period January to March and used to quantify the secondary production in each month on the assumption that it did not change during that period. The temporal dynamics of production did
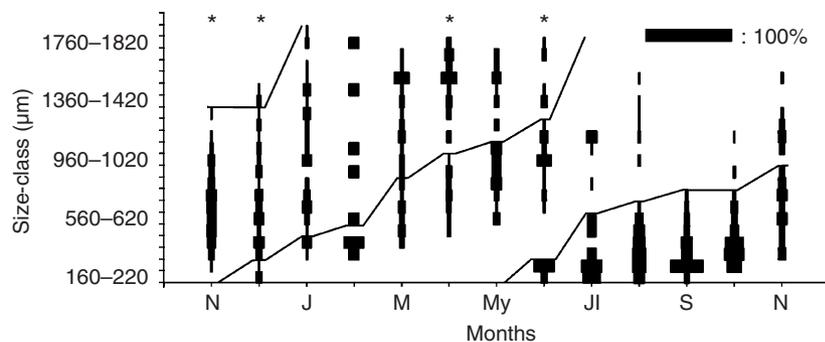

Fig. 2 Size-frequency of *Sericostoma vittatum* larvae from November 2000 to November 2001 in the S. João stream. Width of bars represents percentage of larvae in each size-class on a given sampling date. Lines separate the two cohorts. Asterisks indicate the months in which pupae were found.
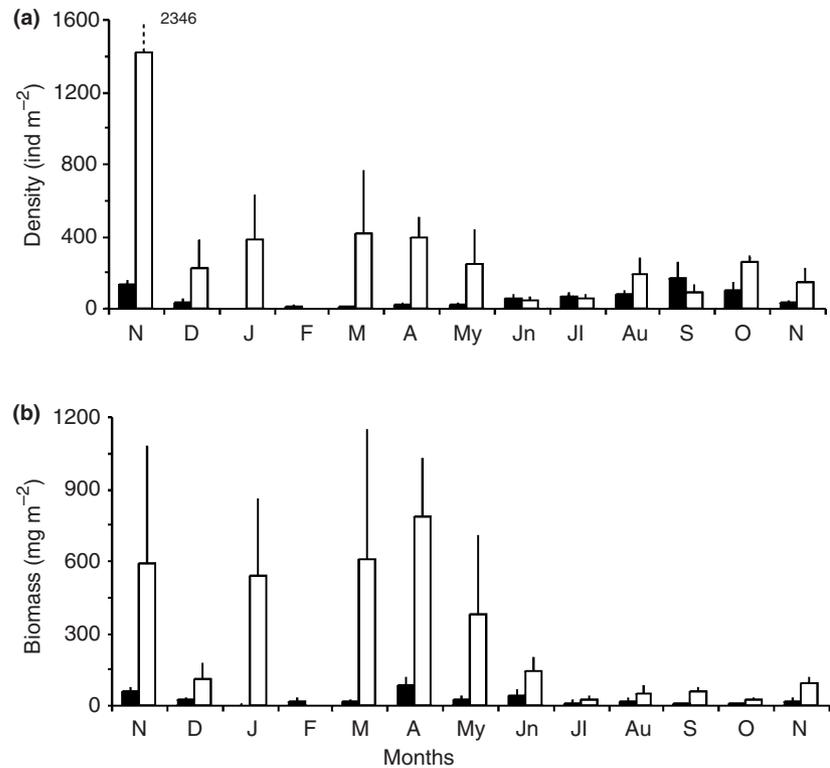
Fig. 3 Temporal patterns of (a) density and (b) biomass of *S. vittatum* larvae in riffles (black columns) and pools (white columns) of the S. João stream. Vertical bars indicate one standard error.

not show clear inter-habitats shifts; lowest values were observed from June to October (Fig. 4).

Feeding and growth experiments

Daily consumption of food in laboratory trials increased geometrically with animal mass (Table 1). Daily consumption also differed among water temperatures and leaf species. For instance, animals fed on chestnut or oak leaves had their highest daily consumption at 18 °C, whereas those fed on alder leaves had their highest daily consumption at 15 °C. Comparisons among daily consumption of poplar leaves were more complex because they were more affected by body mass at 9, 12 and 15 °C than at 18 °C. At 18 °C, daily consumption of animals fed on oak were lower than those of animals fed the other three leaf species (Table 1). At the other temperatures, the slopes of the daily consumption–mass regressions of animals fed on oak were less steep than those of animals fed on poplar.

Based on the results of the feeding experiments, a model in the form $\ln(C) = a + b \ln(M) + cT + dT^2$ was used to predict daily consumption (C) of the four

leaf species by animals having mass (M) at a given water temperature (T, °C). The model assumed that daily consumption of food had a power relationship with animal mass and a parabolic one with water temperature. These equations explained 22–57% of the variability in feeding rates (Table 2) and were highly significant ($P < 0.0001$) for all leaf species. For the range of temperatures tested, the equations predicted higher daily consumption at higher individual mass and temperature. Nevertheless, increases in feeding rates were much smaller when larvae were fed oak than other leaf species (Fig. 5). Moreover, daily consumption of chestnut leaves showed little dependence on temperature when it was lower than 15 °C. Finally, the multiple regressions also predicted that larvae fed on alder and poplar had higher daily consumption than those fed on chestnut and oak (Fig. 5).

Growth was also related to *S. vittatum* mass, but the relationship was expressed best by negative exponential equations (Table 3). The correlation coefficients between growth rate and animal mass were lower than those between daily consumption and mass, but, in general, they were also significant. When animals
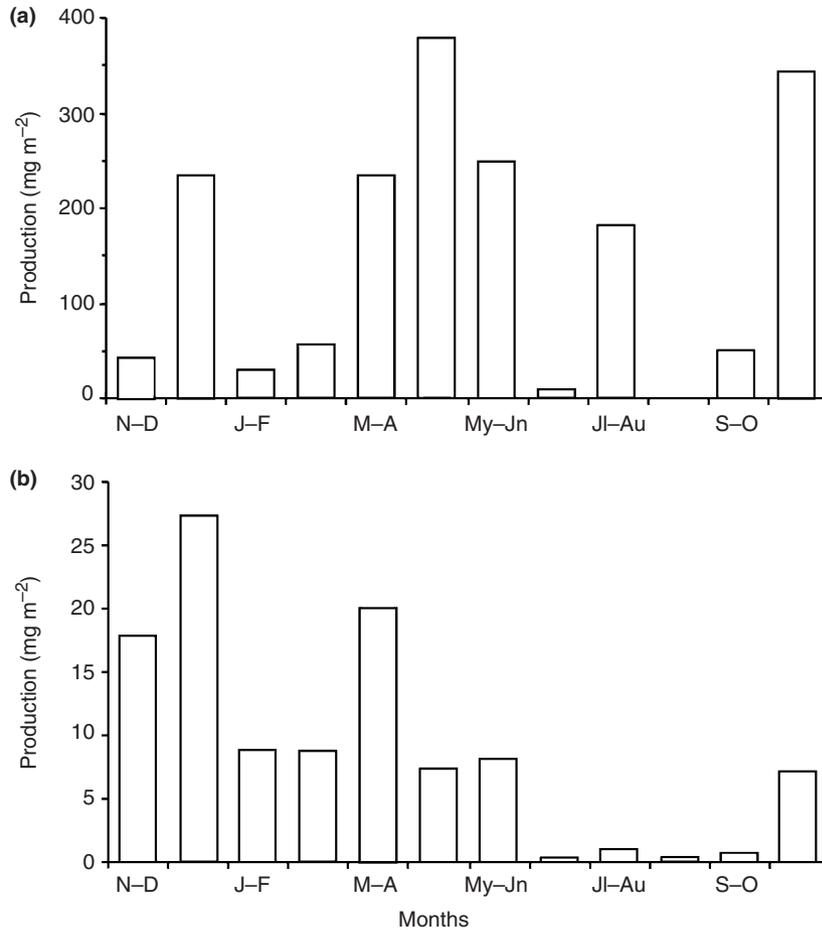
(a)

(b)

Fig. 4 Temporal dynamics of *Sericostoma vittatum* production in riffles (a) and pools (b). Note that the scale for riffles and pools differs.

were fed on chestnut litter, growth rates were higher at 12 and 15 °C than at 9 and 18 °C. When larvae consumed alder, poplar or oak, the slopes of the growth–mass equations varied among temperatures with no general pattern (Table 3). General patterns were not observed either when *S. vittatum* growth rates were compared among leaf species. At 9 °C, the slope of growth–mass relationship differed between alder and oak, but were similar to those of the other two leaf species. At 18 °C, those of animals fed on alder or poplar were highest, those of animals fed on oak litter were lower and those of animals fed on chestnut, the lowest. At 12 and 15 °C, growth rates did not differ among leaf species.

To predict growth rates, a parabolic relationship with water temperature and an exponential relationship with animal mass were assumed. Thus, the model took the form: $\ln(g) = a + bM + cT + dT^2$, where larvae fed on alder, chestnut, poplar or oak.

Growth rates decreased with increasing body mass, and reached their highest values at water temperatures between 13.7 and 16.7 °C (see Table 4). These equations explained 29–47% of the variability in results of growth experiments and were highly significant ($P < 0.0001$). They predicted that growth rates of larvae fed on alder were less mass-dependent than those of larvae fed on the other leaf species tested (Fig. 5). Moreover, larvae that consumed alder had the highest growth rates, whereas growth rates of the animals fed on poplar were slightly higher than those of the animals fed on chestnut or oak (Fig. 5). Note that, although the relationships between instantaneous growth rates (g) and individual mass (M) were negative, the mass gained per day by *S. vittatum* larvae (i.e. gM) increased with increasing individual mass until they reached an individual mass that ranged from 3.2 mg (animals fed on poplar) to 6.4 mg (animals fed on alder).

Table 1 Summary of regression coefficients for estimating daily consumption (C, mg day^{-1}) of *Sericostoma vitttatum* larvae fed on each leaf species at each water temperature tested. Regressions are based on the model $\ln(C) = a + b \ln(M)$, where M is *S. vittatum* mass (mg). Results of the inter-temperature and inter-food comparisons using the Tukey Honestly Significant Difference Test are also shown, with values increasing from right to left. Differences between the slopes or intercepts of the regression lines are indicated. Temperatures or foods linked by a line did not show significant differences

Leaf species	Temperature (°C)	a	b	n	r^2	
Alder	9	−0.792	0.619	67	0.384	***
	12	−1.009	0.581	55	0.445	***
	15	−0.146	0.656	80	0.611	***
	18	−0.294	0.525	93	0.255	***
Chestnut	9	−0.728	0.683	64	0.435	***
	12	−0.529	0.452	42	0.449	***
	15	−0.750	0.829	76	0.645	***
	18	−0.090	0.407	99	0.256	***
Poplar	9	−0.537	0.727	63	0.493	***
	12	−0.558	0.837	53	0.776	***
	15	−0.168	0.762	76	0.624	***
	18	−0.025	0.391	100	0.145	***
Oak	9	−0.903	0.296	67	0.124	**
	12	−1.01	0.351	57	0.123	*
	15	−0.874	0.06	49	0.013	NS
	18	−0.388	0.219	100	0.046	*

NS, not significant ($P > 0.05$); *$P < 0.05$; **$P < 0.005$; ***$P < 0.0001$; Alder: 15 18 9 12 intercepts***; Chestnut: 18 12 9 15 intercepts***; Poplar: 9 15 12 18 slopes**; Oak: 18 15 9 12 intercepts***; 9 °C: poplar chestnut alder oak slopes**; 12 °C: poplar alder chestnut oak slopes**; 15 °C: chestnut poplar alder oak slopes***; 18 °C: poplar chestnut alder oak intercepts***.

Table 2 Summary of regression coefficients for estimating daily consumption (C, mg day^{-1}) of *Sericostoma vittatum* larvae fed four leaf species. Regressions are based on *S. vittatum* mass (M, mg) and water temperature (T, °C). The equations follow the model $\ln(C) = a + b \ln(M) + cT + dT^2$

Leaf species	a	b	c	d	n	r^2
Alder	−2.281	0.526	0.206	0.005	295	0.426
Chestnut	0.974	0.684	−0.307	0.013	281	0.572
Poplar	−2.309	0.679	0.283	0.009	297	0.516
Oak	0.882	0.226	−0.31	0.013	274	0.219

Gross production efficiency of *S. vittatum* larvae depended greatly on the leaf species consumed (Fig. 5). Larvae fed on oak were more efficient in converting consumption to growth than those fed on alder and chestnut, whereas those fed on poplar were least efficient. When food consisted of alder, chestnut or oak leaves, water temperature had a strong influence on GPE, but it was weaker when animals consumed poplar leaves. The GPEs of larvae fed on alder or poplar decreased with increasing temperature, but those of larvae fed on chestnut or oak increased with temperature upto about 13.2 and 14 °C, respectively and decreased thereafter. Animal mass had no consistent effect on GPE either: it was negative when the animals consumed chestnut or poplar, whereas it depended on the individual mass when they were fed on alder or oak.

Leaf litter consumption in the field

Estimated leaf litter consumption was higher in pools than riffles (Fig. 6, Table 5). The annual values for the *S. vittatum* population were highest if the animals were assumed to have fed on poplar leaves, lower if fed on oak or chestnut and lowest if they were assumed to consume alder leaves (Table 5). Food consumption was highest in pools from October to June, whereas in riffles, temporal patterns were not clear (Fig. 6).

Discussion

CPOM stocks

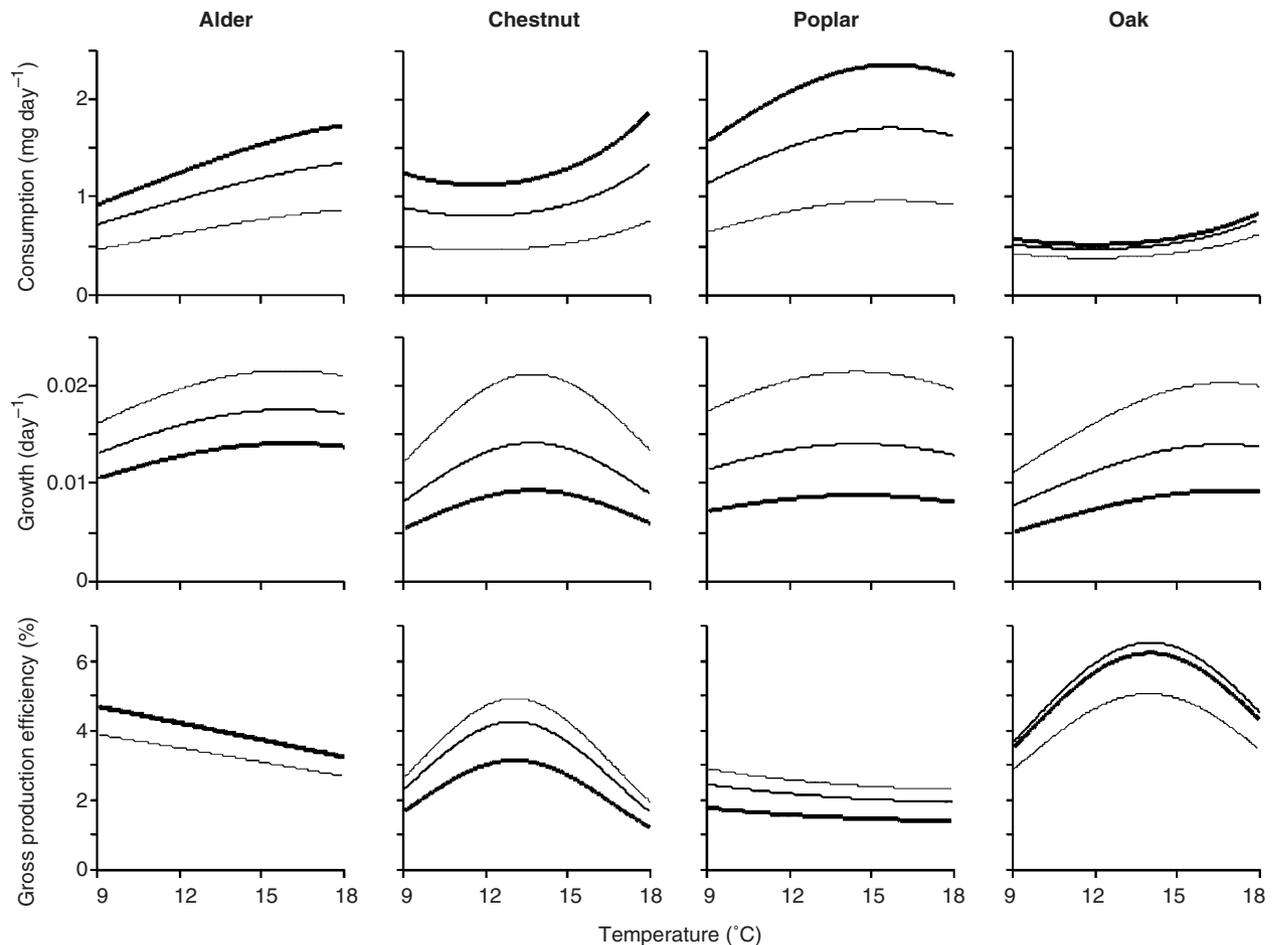Mean standing stocks of CPOM in the S. João stream (6.3 g m^{-2}) were much lower than those reported by

Fig. 5 Daily consumption, growth rate and gross production efficiency of *Sericostoma vittatum* larvae of body mass 1.1 mg (fine line), 2.5 mg (coarse line) and 4 mg (coarsest line) as predicted by water temperature when fed chestnut, poplar and oak leaf litter.

Abelho & Graça (1996) in nearby streams surrounded by deciduous forest (55.8 g m^{-2}). Higher values of CPOM stocks have also been reported in other streams of central Portugal (157 g m^{-2}, Abelho & Graça, 1998) and Northern Spain (20–60 g m^{-2}, González & Pozo, 1996) that also drain deciduous forests. In all the above cited cases, the stream banks were covered completely by deciduous trees, whereas the S. João stream has steep, rocky banks.

Population dynamics

Sericostoma vittatum had two overlapping cohorts in the S. João stream. Other *Sericostoma* sp. have univoltine life histories (e.g. *S. pyrenaicum* Pictet in Northern Spain; González, 2000) and semivoltine life histories are also common (e.g. *S. personatum* Stephens in

central Europe; Iversen, 1980; Wagner, 1990). Some authors have suggested that the life histories of detritivores are keyed to exploit the autumnal pulse of leaf fall, with the major growth period occurring in late autumn and winter (e.g. Anderson & Cummins, 1979; Cowan & Oswood, 1984). However, the presence of two coexisting cohorts with different phenologies in *S. vittatum* does not conform with this suggestion. Other studies have stressed the potential benefits of asynchronous development, which can be viewed as a 'bet-hedging' strategy in unpredictable ambients (e.g. Winterbourn *et al.*, 1981; Sangpradub *et al.*, 1999). This could be also the case of *S. vittatum* in the S. João stream, because the trait of having two different cohorts per year could be advantageous when the floods can cause periods of high mortality of larvae during almost all the year.

Table 3 Summary of regression coefficients for estimating growth rates (g, day^{-1}) of *Sericostoma vittatum* fed four leaf species at four water temperatures. Regressions are based on the model $ln(g) = a + bM$, where M is *S. vittatum* mass (mg). Results of the inter-temperature and inter-food comparisons are also shown, with values increasing from right to left. Differences between slopes or intercepts of the regression lines are indicated. Temperatures or foods linked by a line did not show significant differences

Leaf species	Temperature (°C)	a	b	n	r^2	
Alder	9	−4.054	−0.105	36	0.150	*
	12	−4.416	−0.013	9	0.002	NS
	15	−3.688	−0.137	27	0.269	*
	18	−3.483	−0.302	35	0.573	***
Chestnut	9	−4.334	−0.168	28	0.169	*
	12	−3.166	−0.512	7	0.545	NS
	15	−3.638	−0.252	32	0.277	**
	18	−4.194	−0.239	28	0.189	*
Poplar	9	−3.823	−0.226	30	0.211	*
	12	−3.215	−0.486	9	0.976	***
	15	−3.534	−0.180	25	0.153	NS
	18	−3.411	−0.332	32	0.570	***
Oak	9	−4.011	−0.355	35	0.368	***
	12	−3.713	−0.471	11	0.341	NS
	15	−3.818	−0.108	32	0.065	NS
	18	−3.605	−0.339	33	0.559	***

NS, not significant ($P > 0.05$); *$P < 0.05$; **$P < 0.005$; ***$P < 0.0001$; Alder: 18 15 9 12 slopes*; Chestnut: 12 15 18 9 slopes**; Poplar: 15 9 18 12 slopes*; Oak: 15 18 9 12 slopes*; 9 °C: alder chestnut poplar oak slopes*; 12 °C: NS; 15 °C: NS; 18 °C: poplar alder oak chestnut intercepts***.

Table 4 Summary of regression coefficients for estimating growth rates (g, day^{-1}) of *Sericostoma vittatum* fed each leaf species. Regressions are based on *S. vittatum* mass (M, mg) and water temperature (T, °C). Equations follow the model $ln(g) = a + bM + cT + dT^2$

Leaf species	a	b	c	d	n	r^2	T_{max}
Alder	−5.208	−0.146	0.192	−0.006	107	0.293	16
Chestnut	−8.241	−0.289	0.686	−0.025	95	0.38	13.7
Poplar	−4.975	−0.308	0.203	−0.007	96	0.472	14.5
Oak	−6.398	−0.272	0.335	−0.01	111	0.332	16.7

T_{max}: temperature at which the the highest growth rates are predicted [calculated as $-c/(2d)$].

Both the abundance and production of this species were higher in pools than in riffles. A similar pattern was found by Huryn & Wallace (1987) and Wohl *et al.* (1995) when comparing shredder production in riffles and pools. They explained the difference in production as a consequence of higher leaf litter deposition in pools than in riffles. Nevertheless, although higher CPOM stocks were observed in pools than in riffles in the S. João stream, no correlation between *S. vittatum* and detritus abundance was found. Thus, the spatial differences in abundance and production observed could have been a consequence of larval responses to other environmental factors (e.g. hydraulics, substratum particle size; see Minshall, 1984 for a review). More information on the habitat preferences of *S. vittatum* is needed to explain the spatial patterns observed in this study.

The secondary production estimates we obtained for riffles and pools are likely to be reliable as they were obtained with two independent methods involving different approaches (for a revision see Benke, 1993). The value found for the S. João stream (441 mg m^{-2} year^{-1}) was among the ranged values reported for shredder invertebrates by Benke (1993). It was higher than that of *S. pyrenaicum* in a Northern Spain stream (89 mg dry mass m^{-2} year^{-1}, González, 2000) but lower than values estimated for *S. personatum* in two Danish streams (802–821 mg m^{-2} year^{-1}, Iversen, 1980). The P/B ratios (4.9–5 year^{-1}) were higher than those found by Iversen (1980) (2–3 year^{-1}), but lower than that recorded by González (2000) (7.2 year^{-1}). Nevertheless, great care is required when analysing production figures for the whole stream benthos, because it has been assumed that the values obtained in pools with sandy bottoms (17% of all pools) were representative of all the pools, irrespective of their bed composition. Such uncertainty does not apply
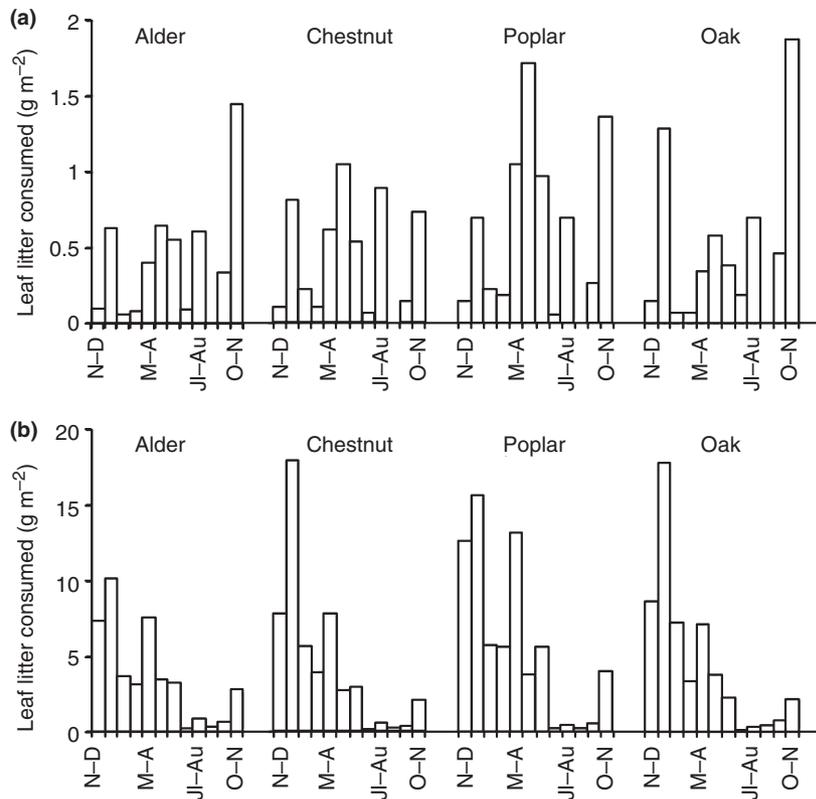
Fig. 6 Amount (g m^{-2}) of alder, chestnut, poplar or oak leaves predicted to be consumed by *Sericostoma vittatum* larvae in riffles (a) and pools (b) of the S. João stream. Note that the scale varies for each habitat.

Table 5 Estimates of the amount of leaf litter consumed (g m^{-2}) by *Sericostoma vittatum* in riffles, pools and the whole bed of the S. João stream during the study period

	Riffles	Pools	Total
Alder	4.99	43.49	14.11
Chestnut	5.24	51.58	16.22
Poplar	7.36	66.93	21.47
Oak	6.10	53.54	17.35

to the P/B ratios, which did not differ between habitats.

Temporal patterns of production observed in this study were related to the life history of *S. vittatum* because during the period with lowest production (June to October), the bulk of the population consisted of very small larvae in cohort 2 and medium-sized larvae in cohort 1. This resulted in low biomass during summer and, as a consequence, low production. The bioenergetic data gathered in our study suggest that annual changes in water temperature had less direct influence on the temporal dynamics of production than the life history because temperatures recorded in summer (Fig. 1) would have allowed

similar or higher growth rates than those recorded in winter (Fig. 5).

Effects of temperature and animal mass on feeding and growth

Temperature increased daily consumption by *S. vittatum*, a pattern shown by other detritivorous caddisflies (e.g. Iversen, 1979; Nolen & Pearson, 1993). It is generally assumed that the relationship between temperature and consumption rates is linear (e.g. Buzby & Perry, 2000), but our results and those of Iversen (1979) with *S. personatum* larvae indicated a non-linear increment of consumption rate with increasing temperatures.

Reports of the effect of water temperature on individual growth rates of freshwater invertebrates are common in the literature (e.g. Huryn & Wallace, 1986; Benke *et al.*, 1992). Most reports predict a positive relationship between growth and temperature over the whole range of temperatures tested (e.g. Lillehammer, 1985; Rosillon, 1988), whereas other studies have found that the effect of temperature on growth rates is positive up to a threshold value and

negative beyond it (e.g. Sutcliffe *et al.*, 1981; Pritchard & Berté, 1987). The results of our work agree with those of the latter authors, and indicate that the optimum temperature for *S. vittatum* growth in S. João stream was between 13.7 and 16.7 °C. Iversen (1979) measured assimilation and respiration rates of *S. personatum* larvae and found that at temperatures above 13 °C, the increase in consumption was not able to compensate for the increase in metabolic costs and hence larval growth decreased. Such a mechanism could also be operating in *S. vittatum* and could explain why production efficiencies estimated in the present study decreased with increasing temperature above 14 °C, irrespective of food type.

As in other studies (Iversen, 1979; Feio & Graça, 2000), the effect of mass on daily consumption was positive, but negative on growth rates. Increasing mass implies increasing metabolic costs, which may be the reason for increasing energy uptake (i.e. higher consumption) but a decrease in the energy available for growth. Because diet influenced the strength of the link between animal mass and feeding and growth rates, the effect of mass on production efficiency depended on the leaf species consumed by the larvae.

Effect of diet on feeding and growth

Larvae fed on two fast-decomposing species (i.e. alder and poplar) had higher daily consumption and growth rates than larvae fed on chestnut and oak leaves. Canhoto & Graça (1995) and Hutchens *et al.* (1997) also reported that the growth rates of detritivores were highest when kept with the leaf species that they consumed more. In contrast, Anderson & Cummins (1979) found that detritivores may increase their feeding rates on low-quality leaf litter in order to maintain growth rates. The latter condition was found by Friberg & Jacobsen (1999), who observed that feeding rates of *S. personatum* on *Picea sitchensis* (Bong.) Carr. (sitka spruce), *Fraxinus excelsior* L. (ash), alder and the filamentous alga *Microspora* sp. correlated inversely to their quality. Our experiment and that of Friberg & Jacobsen (1999) differed in (a) the nature of the food consumed by the caddis-flies (green leaves or needles conditioned for 1 month and senescent leaves conditioned for 2 weeks, respectively), (b) the *Sericostoma* sp. studied, and (c) in the results obtained (lower feeding rates in their case). It is possible to hypothesise that inter-experiment dif-

ferences in the caddis species used and in the quality of food items offered to the larvae could have made the results of the experiments differ, but more information is importantly needed to identify the factors involved.

As with feeding and growth, production efficiency varied greatly not only with water temperature and animal mass but also with the leaf species offered as food. Values obtained in this experiment were in the low range of those reported in other studies on detritivore energetics (e.g. Jacobsen & Sand-Jensen, 1994; Hutchens *et al.*, 1997). They were higher than those calculated for *S. personatum* fed on *Fagus sylvatica* L. (beech) (Iversen, 1979) or sitka spruce (Friberg & Jacobsen, 1999) litter, but lower than those exhibited by *S. personatum* larvae fed alder or ash leaf litter (Friberg & Jacobsen, 1999). It must be noted again that these authors fed the caddis-flies with green leaves, which can be more palatable to invertebrates than naturally abscised ones (Boulton & Boon, 1991).

Food consumption in the field

Our estimates of the amount of leaf litter consumed by *S. vittatum* per year in the S. João stream (14–21 g m^{-2}) were much lower than the value reported by Iversen (1980) for a *S. personatum* population in a beech forest stream (50 g m^{-2}, AFDM). Nevertheless, our results are roughly similar to the 25 g m^{-2} (dry mass) of *Q. robur* litter consumed by limnephilid caddis-flies in a woodland pond in Switzerland (Oertli, 1993) and the 30 g m^{-2} (AFDM) of CPOM ingested by another limnephilid (*Ironoquia plattensis* Alexander & Whiles) in a slough surrounded by meadows in Nebraska (Whiles *et al.*, 1999).

Whereas Whiles *et al.* (1999) reported that *I. plattensis* consumed 13% of the mean annual CPOM stock in the study site, the consumption values for *S. vittatum* represented 2.3 to 3.4 times the mean annual CPOM standing stock in the S. João stream. Our results indicate therefore that high detritus turnover rates are necessary to allow such consumption values and suggest that the detritivore guild was food limited in the S. João stream, as at other sites (e.g. Richardson, 1991; Dobson & Hildrew, 1992).

Our results indicate that realistic estimates of leaf litter mass consumed need to take into account the variability in growth performance because of diet.

This aspect of aquatic insect energetics has been neglected in the literature, but our study has shown that to maintain the production of *S. vittatum* in S. João stream, 53% more leaf litter mass would be needed if all the leaves were poplar than if they were alder. Moreover, if the production efficiency data given by the above-cited authors (9% in Oertli, 1993; 5% in the other cases) had been used for *S. vittatum*, our estimates of leaf litter consumed would had been 4.9–8.8 g m^{-2}, respectively; i.e. only 34–62% of the lowest value calculated for the S. João stream population.

The present study has shown that temporal patterns of food consumption by *S. vittatum* were not linked to changes in water temperature or CPOM stocks, but to the individual mass of larvae and thus their life history. Leaf consumption, growth rate, and the production efficiency of a given *S. vittatum* larva were dependent on its mass. Furthermore, the period of highest production (and hence highest leaf litter consumption) occurred when larvae attained their maximum individual mass and started to pupate. Our results highlight the need for taking into account the size-structure of populations in order to estimate their role in ecosystem energetics with greater precision.

Acknowledgments

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