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## Research Paper

# *Sericostoma vittatum* (Trichoptera) Larvae Are Able to Use Pine Litter as an Energy Source

*key words:* shredders, growth, consumption, conifer, litter processing

### Abstract

We tested the effect of conditioning time of *Pinus sylvestris* litter on food consumption and growth of laboratory-reared *Sericostoma vittatum* larvae. In all cases, larval mass was positively correlated with consumption rates but negatively with growth rates and gross production efficiencies. Conditioning time (4, 8 or 30 weeks) had an effect on feeding rates: they were lowest for the least conditioned pine litter, but no effect of conditioning time on growth rates was observed. Contrary to previous reports on conifer litter use by aquatic detritivores, our results indicate that *S.vittatum* larvae were able to transform the highly refractory pine litter into secondary production even when it was conditioned for only 4 weeks.

### 1. Introduction

Leaf litter from riparian vegetation is the main energy source in small streams where canopy limits periphyton production (FISHER and LIKENS, 1973; WALLACE *et al.*, 1999). After the leaf litter enters the stream, it is colonized and consumed by both microorganisms and detritivore invertebrates (MERRITT *et al.*, 1984; GESSNER *et al.*, 1999). This process is a central issue in stream functioning because it transforms litter into materials available to other components of the stream community: microbial and animal biomass and other forms of detritus, *e.g.*, faeces and small detritus particles, that may be exported downstream (WALLACE and WEBSTER, 1996; GRAÇA and CANHOTO, 2006).

Physical and chemical characteristics of leaves greatly differ among tree species (KILLINGBECK, 1996; OSTROFSKY, 1997) affecting invertebrate feeding and growth rates (ANDERSON and SEDELL, 1979; GRAÇA, 2001). Leaf litter toughness may decrease or even impede detritivore feeding, particularly in the case of initial instars (NOLEN and PEARSON, 1993; FEIO and GRAÇA, 2000). Nutrient concentrations in leaf tissues, however, increase detritivore feeding and growth rates (IRONS *et al.*, 1988; CANHOTO and GRAÇA, 1995). Litter traits change during litter breakdown (for a review, see GESSNER *et al.*, 1999 and ABELHO, 2001) due to (1) changes in the proportions of labile and recalcitrant substances, (2) release of a variable amount of soluble chemicals (leaching) and (3) modification of chemical and physical characteristics of detritus by microbial colonization and activity (conditioning).

Microbial conditioning enhances the quality of detritus for detritivores (*e.g.*, GRAÇA *et al.*, 2001; BASTIAN *et al.*, 2007) due to an array of factors. First, invertebrate consumers assimilate

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late better microbial biomass on conditioned leaves than leaf tissues (MERRITT *et al.*, 1984). Secondly, microorganisms produce enzymes that transform non-assimilable compounds into simple molecules easily used by invertebrates (JENKINS and SUBERKROPP 1995; CANHOTO *et al.*, 2002). Such enzymes may remain active after litter ingestion (CUMMINS and KLUG, 1979; BÄRLOCHER, 1985), increasing the benefits to detritivores of feeding on conditioned leaves. Finally, microbial activities soften litter, making easier the ingestion of leaf tissue by invertebrates (GRAÇA *et al.*, 1993; GESSNER *et al.*, 1999).

Here we analyzed the use of senescent litter of *Pinus sylvestris* L. (pine) by the shredder caddisfly *Sericostoma vittatum* RAMBUR. We hypothesized that, due to the low initial quality of detritus, larvae fed on poorly-conditioned pine litter would have slow growth and low survival, gross production efficiency and feeding rate. Litter conditioning would make these parameters higher.

*P. sylvestris* has a very broad Palearctic distribution (CRITCHFIELD and LITTLE, 1966), including mountains of Central Spain, where forest management has replaced montane riparian trees, such as *Betula pubescens* EHRH., *Populus tremula* L. and *Salix atrocinerea* BROT., by pine in many stream banks (FERNÁNDEZ-GONZÁLEZ, 1991). *P. sylvestris* senescent needles are regarded as low quality detritus because they are tough, nutrient-poor and have chemicals toxic for invertebrates (MC TIERNAN *et al.*, 2003; SARIYILDIZ, 2003). Thus, we aimed to test if this vegetation change could affect invertebrate feeding on allochthonous detritus which could impair stream function.

The studied detritivore is *S. vittatum*, a caddisfly well-distributed in streams of Iberian Peninsula (GONZÁLEZ *et al.*, 1992). *Sericostoma* spp. can be found in most Europe (MALICKY, 2004) and it has been used in many experiments that measure mortality, feeding and growth rates, assimilation and gross production efficiency and food preferences when fed with different items including leaf litter detritus (IVERSEN, 1974, 1979; WAGNER, 1990; FRIBERG and JACOBSEN, 1994, 1999; FEIO and GRAÇA, 2000; GRAÇA *et al.*, 2001; GONZÁLEZ and GRAÇA, 2003; CARVALHO and GRAÇA, 2007). This bulk of previous information allows putting into a much broader context the performance of *Sericostoma* larvae eating pine needles.

## 2. Methods

In this study we measured (1) feeding rate, (2) growth rate and (3) gross production efficiency of the shredder caddisfly *S. vittatum* fed pine litter conditioned for 4, 8 or 30 weeks in three separate experiments. In each experiment, 20 *S. vittatum* larvae were kept during 4 weeks in individual 25 ml glass flasks with aeration provided by an air pump, calcinated fine sand, stream water and a known mass of pine needles. Flasks were inside a germination chamber with constant temperature, 15 °C, and photoperiod 12/12 hours.

### 2.1. Litter and Larvae Collection, Processing and Storage

All *P. sylvestris* needles used in the experiments were collected on 15th November 2006 at a pine forest in Guadarrama Mountains, Central Spain (40°42'35" N 04°08'28" W) at roughly 1500 m a.s.l. Only yellow-brownish, senescent needles tangled in twigs of trees and shrubs were selected. Those needles damaged by herbivores were discarded. Leaf litter was air-dried in the laboratory and stored at ambient temperature in a cardboard box until needed.

The *S. vittatum* larvae were collected from a 100 m reach of the Hoyo Cerrado stream (Guadarrama Mountains, 40°52'35" N, 03°54'55" W). The animals were transported to the laboratory inside a cooling box. Forty nine larvae were used to construct a size-mass equation to know dry mass of larvae (excluding case) from the maximum width of their cases. This last parameter was measured with a micrometer fitted to a stereomicroscope (precision 50 µm); the larvae were extracted from their cases, put individually on pre-weighed aluminum foils, killed and dried in an oven at 60 °C until constant mass. Then, the

aluminum foils were reweighed (precision 0.1 mg) to know the dry mass of each larva. Larvae used in the feeding experiments were kept at plastic containers with leaf litter from the stream and aeration that were inside the germination chamber at controlled environment of 15 °C, 12/12 photoperiod.

## 2.2. Litter Conditioning

A plastic container with wood pieces, pine bark and 40 l of water from the Hoyo Cerrado stream and aeration was kept in a germination chamber at the above indicated conditions. Twelve groups of 400 needles were put into labeled PVC tubes with both ends covered with 0.5 mm mesh that were submerged in the 40 l container at scheduled times to get 4, 8 or 30 weeks-conditioned litter for the 4 weeks of each experiment.

## 2.3. Measurement of Consumption Rates

*P. sylvestris* needles grow in pairs attached by their basis. After incubation, we separated the 2 needles of each pair with a cut near their basis obtaining 2 apical fragments of the same length. In the experiments, each animal received weekly 10 needle fragments, the other 10 fragments, from the same 10 needle pairs, were dried (60 °C, 48 hours) and weighted (precision, 0.1 mg) to estimate initial mass of food offered to each animal (mean: 0.06 g). A previous trial had shown that mean difference of dry mass between the heaviest and the lightest groups of 10 needle fragments from the same pairs was small (3.82% for 17 pairs).

Each feeding trial lasted 1 week; at the end of each week, the needle fragments remaining at each flask were collected, dried and weighted before changing the water and adding new sand and new detritus. These feeding trials were repeated 4 times for each incubation time.

Following IVERSEN (1974), feeding rates were calculated as:

$$FR = (M_t - M_i)/t$$

where "FR" is feeding rate (g day<sup>-1</sup>); "M<sub>t</sub>" is mass of the needle remains found at each flask after a week (g); "M<sub>i</sub>" is mass of the 10 needle fragments cut from the same needle pairs that those offered to the larva (g) and "t" is the duration of each feeding trial (days, precision 1 minute). No attempt was done to measure microbial activity in pine litter because we assumed that mass loss due to microorganisms would be hardly detectable compared to mass of detritus ingested by the animals. The feeding rates reported in this paper include thus an amount of mass loss due to microorganisms.

## 2.4 Measurement of Growth Rates

The case diameters of larvae were measured at the start of the experiments and each week afterwards, allowing obtaining larval mass using the size-mass regression model. Because case diameter of many larvae did not increase in a week, growth was calculated from the diameter increment in 3 weeks. Since the animals were fed with the same kind of detritus for 4 weeks, we took weekly measurements and calculated 2 growth rate measures: from day 0 to day 21 and from day 7 to day 28. Daily instantaneous growth rates (DIGR, day<sup>-1</sup>, hereafter daily growth, BENKE, 1993) were calculated as:

$$DIGR = (\ln(L_t) - \ln(L_i))/t$$

where "L<sub>t</sub>" is mass of each larva at day 0 or day 7 (g); "L<sub>t</sub>" is mass of each larva 3 weeks later and "t" is elapsed time (days, precision 1 minute).

## 2.5. Calculation of Gross Production Efficiency

Gross production efficiency (hereafter, production efficiency) was calculated as rate of larval mass increment in 3 weeks (g day<sup>-1</sup>) divided by mean feeding rate in those 3 weeks (g day<sup>-1</sup>). Mass increment of larvae was measured as mass (g) gained in 3 weeks of experiment (days). Feeding rate of larvae

were calculated as the mean of the 3 feeding rates measured during the 3 weeks, corrected with the time used to obtain each feeding rate. The larvae that pupated during the experiments were replaced with new animals of similar mass, but those feeding rates and daily growth recordings that included the week when the animal pupated were not recorded.

## 2.6. Data Analysis

Size-mass equation was obtained using simple linear regression with case diameter (C) as predictor variable and larval mass (L) as response variable. We constructed linear ( $L = a + b \times C$ , where "a" and "b" are regression constants), exponential ( $L = a \times e^{bC}$ ) and power ( $L = a \times C^b$ ) models to fit our data. In all the cases, the models were obtained using the least-squares method with log transformation of variables when needed. The raw residuals of the models were plotted against case diameter to detect if the assumption of homogeneity in the variance was met and check if the variables had non-linear relationship (QUINN and KEOGH, 2002).

All the other parameters calculated in this paper (feeding rate, daily growth and production efficiency) may also depend on individual mass. These results were analyzed following the above indicated method. Simple linear regressions of these parameters including larval mass as predictor variable were, thus, constructed assuming linear, exponential and power relationships and raw residuals were examined before selecting the most accurate equation.

Some exceptionally deviant values of feeding rates were observed. They were attributed to (1) experimental errors involving case measurement and collection, drying and weighting of detritus and (2) occurrence of uncontrolled events during the experiments such as larval molting and variations in palatability of pine needles that can alter the results. Consequently, we calculated standardized residuals following SOKAL and ROHLF (1995) and, when they were greater than  $t_{0.05, n-2}$ , where "n" is the number of data, the original observation was considered as an outlier. When outliers were detected, new models excluding those suspicious data were constructed.

The effect of conditioning time of litter on feeding rate, daily growth and production efficiency was assessed following ZAR (1996). First, the slopes of the models were compared among them and, for those equations with similar slopes ( $P > 0.05$ , test of homogeneity of slopes), a test of homogeneity of intercepts was also used. If differences between the 3 slopes or the 3 intercepts were found, post hoc comparisons were performed with the corresponding Tukey test. Additionally, when differences among slopes were found, the Wilcoxon modification of the Johnson-Newman procedure (WILCOX, 1987) was used to determine the range of individual mass over the diet is associated to significant differences in the response variable. This test (hereafter, Wilcoxon test) was performed using the Wilcoxon.exe program written by A. CONSTABLE (QUINN and KEOGH, 2002). The regressions, diagnoses of residuals and tests of homogeneity of slopes and intercepts were performed with SPSS 14.0; for outlier detection and Tukey tests, ad-hoc templates were constructed using Excel 2003.

When we had to compare the daily growth rates found in this study (DIGR,  $\text{day}^{-1}$ ) with growth rates calculated by other authors in terms of  $\% \text{ day}^{-1}$  (PGR), we transformed the units of their results into  $\text{day}^{-1}$  using the equation:

$$\text{DIGR} = (\ln(1 + t \times \text{PGR}/100))/t$$

where t is time (days) to obtain the PGR.

## 3. Results

The relationship between case diameter and mass of *S. vittatum* larvae was described best by the power model:

$$\ln(L) = -25.226 + 2.599 \times \ln(C), \quad n = 49, \quad r^2 = 0.45, \quad P < 0.0001$$

where "L" is mass of the larva (g) and "C" is case diameter ( $\mu\text{m}$ ).

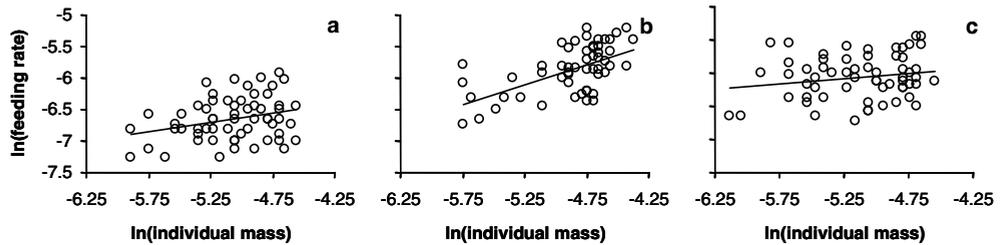


Figure 1. Relationship between individual mass (g) of *S. vittatum* larvae and their feeding rate ( $\text{g day}^{-1}$ ) on pine litter conditioned for 4 (a), 8 (b) and 30 weeks (c). Note that both axes are in log scale.

The amount of pine litter given to the larvae did not limit detritivore performance because after all feeding trials, most of pine detritus was not consumed but remained in the flasks. All the animals used in the experiments survived; 15 larvae pupated.

Individual mass of larvae were positively related to feeding rates by power models (Fig. 1, Table 1). Conditioning time of pine litter had significant effect on the increase of feeding rate with individual mass ( $P < 0.005$ , test of homogeneity of slopes). The slope of the equation constructed for litter conditioned 8 weeks was higher than the slopes of the equations constructed for the other conditioning times ( $P < 0.01$ , Tukey test for slopes), which did not differ between them ( $P > 0.05$ , Tukey test for slopes). Moreover, intercept of the equation for animals fed on 30 weeks conditioned litter was higher than that of the equation for animals eating pine conditioned 4 weeks ( $P < 0.0001$ , test of homogeneity of intercepts). This last result means that, discounting the effect of mass, the larvae of *S. vittatum* showed higher feeding rate on pine litter conditioned for 30 weeks than on pine conditioned for 4 weeks.

For the total range of individual mass, larvae fed on 8 weeks conditioned litter had higher feeding rates than those that consumed 4 weeks conditioned litter ( $P < 0.05$ , Wilcox test). However, difference on feeding rates between animals eating 8 weeks conditioned litter and

Table 1. Summary of the regression models found for the relationship between mass of *S. vittatum* larvae (M, g) and their feeding rate (FR,  $\text{g day}^{-1}$ ), daily instantaneous growth rate (DG,  $\text{day}^{-1}$ ) and gross production efficiency (PE). *n.s.*: no significant. The slopes and the intercepts with no differences between them have the same superscript.

Conditioning time (weeks)	<i>n</i>	$r^2$	<i>P</i>	model	Range of mass (g)
4	58	0.074	<0.05	$\ln(\text{FR}) = 0.280^{\text{A}} \ln(\text{M}) - 5.359^{\text{X}}$	0.0028 – 0.0106
8	53	0.446	<0.0001	$\ln(\text{FR}) = 0.765^{\text{B}} \ln(\text{M}) - 2.144$	0.0032 – 0.0126
30	58	0.100	<0.05	$\ln(\text{FR}) = 0.259^{\text{A}} \ln(\text{M}) - 4.749^{\text{Y}}$	0.0022 – 0.0106
4	25	0.398	<0.001	$\text{DG} = -2.013^{\text{A}} \text{M} + 0.024^{\text{X}}$	0.0026 – 0.0092
8	26	0.367	<0.001	$\text{DG} = -1.901^{\text{A}} \text{M} + 0.025^{\text{X}}$	0.0032 – 0.0106
30	26	0.292	<0.005	$\text{DG} = -2.821^{\text{A}} \text{M} + 0.021^{\text{X}}$	0.0022 – 0.0087
4	25	0.058	<i>n.s.</i>	$\text{PE} = -3.415^{\text{A}} \text{M} + 0.082^{\text{X}}$	0.0026 – 0.0092
8	26	0.237	<0.05	$\text{PE} = -4.842^{\text{A}} \text{M} + 0.071^{\text{Y}}$	0.0032 – 0.0106
30	26	0.003	<i>n.s.</i>	$\text{PE} = -0.594^{\text{A}} \text{M} + 0.032^{\text{Y}}$	0.0022 – 0.0087

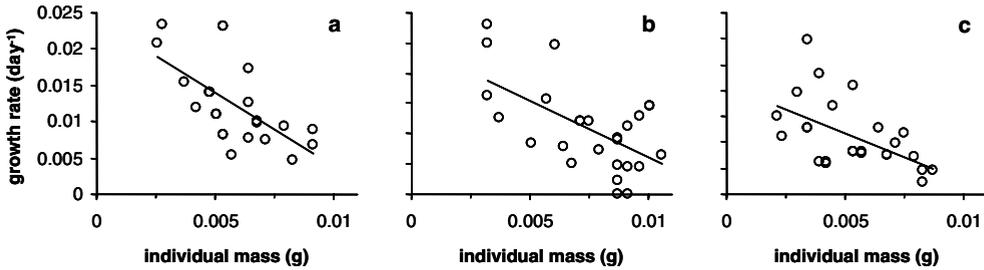


Figure 2. Relationship between individual mass (g) of *S. vittatum* larvae and their daily growth (day<sup>-1</sup>) on pine litter conditioned for 4 (a), 8 (b) and 30 weeks (c).

animals eating 30 weeks conditioned litter was not significant if animal mass was lower than 0.0081 g.

Daily growth was also related to individual mass, but in this case the relationship was linear and the slopes were negative (Table 1, Fig. 2). No effect of conditioning time of litter was detected on daily growth ( $P > 0.05$ , test of homogeneity of slopes and test of homogeneity of intercepts).

Gross production efficiency was related to individual mass by linear models, but such a relationship was only significant for animals eating 8 weeks conditioned litter (Table 1). However, the slope for the pooled production efficiencies (*i.e.*, animals eating 4, 8 and 30 weeks conditioned pine) was significant ( $P < 0.05$ , linear regression). Again, the production efficiency of big larvae was lesser than that of small ones (Fig. 3). Conditioning time of litter had not significant effect on the slope of larval mass on production efficiency ( $P > 0.05$ , test of homogeneity of slopes). However, animals fed on 4 weeks conditioned litter had higher production efficiency than animals of the same size fed on pine conditioned for 8 and 30 weeks ( $P < 0.005$ , Tukey test for intercepts). No difference was observed between the production efficiency of larvae fed on 8 and 30 weeks conditioned litter ( $P > 0.05$ , Tukey test for intercepts).

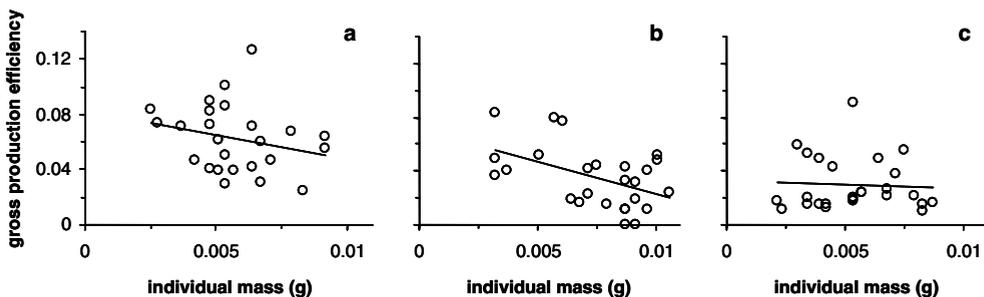


Figure 3. Relationship between individual mass (g) of *S. vittatum* larvae and their gross production efficiency on pine litter conditioned for 4 (a), 8 (b) and 30 weeks (c).

## 4. Discussion

### 4.1. Effects of Body Mass

As in previous experiments with *Sericostoma* spp. (IVERSEN, 1979; GONZÁLEZ and GRAÇA, 2003), feeding rate of larvae increased with body mass, a result that can be explained by greater body mass causing higher total energy demands (e.g., GRAFIUS and ANDERSON, 1980; PERRY *et al.*, 1986). This rise in energy needs must be accounted for increasing food consumption rate and/or assimilation efficiency. We did not measure assimilation efficiency of *S. vittatum* larvae, but IVERSEN (1979) found that for *S. personatum* larvae fed on *Fagus sylvatica* leaves, it was unrelated to body mass. Moreover, the general trend among arthropods shows a decreasing assimilation efficiency with development (SCRIBER and SLANSKY, 1981). The increment in body mass seems, thus, may have forced the larvae to raise the ingestion rates to satisfy their metabolic costs and obtain the energy needed to grow.

As in other experiments (e.g., PERRY *et al.*, 1986; GONZÁLEZ and GRAÇA, 2003), the relationship found between individual mass and feeding rate was not linear. This result suggests that pooling the feeding rates of larvae of differing sizes may be questionable even if units of mass of food eaten per mass of animal are used (e.g., ANDERSON and GRAFIUS, 1975; GRAFIUS and ANDERSON, 1980).

The inverse relationship between body mass and daily growth found in this study has been reported in other papers (e.g., PERRY *et al.*, 1986; GONZÁLEZ and GRAÇA, 2003) and it is also the general trend for immature arthropods (SCRIBER and SLANSKY, 1981). It must be noted here that low daily growth ( $\text{day}^{-1}$ ) does not necessarily mean low mass increment per day ( $\text{g day}^{-1}$ ): larvae showing the highest daily mass gain ( $\text{g day}^{-1}$ ) were the medium-sized ones. Gross production efficiency was not related to body mass in 2 out of 3 experiments. In the literature, this parameter shows variable, if any, relationship with body mass (e.g., IVERSEN, 1979; SCRIBER and SLANSKY, 1981; PERRY *et al.*, 1986).

### 4.2. Effects of Conditioning Time

The results of these experiments only partially fulfilled our hypothesis on feeding rate: *S. vittatum* larvae did show the lowest feeding rate on needles conditioned for 4 weeks. However, depending on the animal mass, feeding rates on litter conditioned during 8 weeks were similar to, or higher than, those on litter conditioned 30 weeks. This means that by 8 weeks pine needles were already fully conditioned.

A positive effect of conditioning of detritus on detritivore feeding rate is commonly reported in the literature (e.g., *Alnus* sp. in ANDERSON and GRAFIUS, 1975; *Acer rubrum* in GOLLADAY *et al.*, 1983; *Acer saccharum* and *Ulmus americana* in BIRD and KAUSHIK, 1985; *Populus tremuloides* in ARSUFFI and SUBERKROPP, 1986; *Ulmus procera* in GRAÇA *et al.*, 1993; *Apodytes brachystylis*, *Crypocarya leucophylla* and *Endiandra bessaphila* in BASTIAN *et al.*, 2007, but see *Freyinetia scandens* in NOLEN and PEARSON, 1993). However, longer conditioning time not always results in increased feeding rates (e.g., *Robinia pseudoacacia* in GOLLADAY *et al.*, 1983; *Carya glabra* in LAWSON *et al.*, 1984; this work). Some reasons can explain this lack of effect. First, because fungi and detritivores compete for the same resource (BÄRLOCHER, 1980; GESSNER *et al.*, 1999), leaf litter may be “over-conditioned” (*sensu* ANDERSON and SEDELL, 1979) after long time exposed to microorganisms, which may result in substrates rich in recalcitrant compounds and, therefore, decreased palatability to invertebrates. Second, some detritivores experimentally exposed to low quality food increase their feeding rates to satisfy their energy and nutrient demands. This “compensatory feeding” has been reported in several studies (e.g., IVERSEN, 1974; ANDERSON and CUMMINS, 1979; GRAFIUS and ANDERSON, 1980; FRIBERG and JACOBSEN, 1999; ALBAR-

IÑO and BALSEIRO, 2001) but not in others (e.g., ARSUFFI and SUBERKROPP, 1986; SMOCK and MCGREGOR, 1988; GRAÇA *et al.*, 1993; JACOBSEN and SAND-JENSEN, 1994; HUTCHENS *et al.*, 1997; GONZÁLEZ and GRAÇA, 2003; this work). In the context of the effects of litter conditioning, compensatory feeding could lead to higher feeding rates on low quality (*i.e.*, low conditioned) detritus.

In our experiment, the occurrence of over-conditioning after 30 weeks of microbial establishment cannot be proved or discarded because the biological, physical and chemical characteristics of decomposing needles have not been measured. Nevertheless, we noticed that by week 30, needles remained rigid with no signals of tissue loss. Thus, we interpret our results as a suggestion that 8 and 30 weeks of conditioning were adequate for maximum or near to maximum feeding rates of *S. vittatum* on pine litter.

The need of long conditioning times to coniferous litter being an adequate substrate for detritivore colonization, feeding and growth is commonly cited in the literature (e.g., ALBARIÑO and BALSEIRO, 2002; COLLEN *et al.*, 2004). In a laboratory experiment, ALBARIÑO and BALSEIRO (2001) found no growth (nor survival) of a detritivore stonefly fed on 15 days conditioned *Pinus ponderosa* needles. Moreover, GRAFIUS and ANDERSON (1980) reported that the shredder caddisfly *Lepidostoma unicolor* was unable to grow if it was fed on needles of *Pseudotsuga menziesii* conditioned for 5 months. Our results, however, do not support the same assertion for *S. vittatum* consuming *P. sylvestris* needles: they showed measurable growth even when they ate needles conditioned in the laboratory for 4 weeks. Moreover, daily growths found in this work were independent on the conditioning time, a result that is against our initial hypothesis of a positive effect of this parameter on growth rates.

Our findings are consistent with the results of GRAÇA *et al.* (2001) who measured growth rates of 4 detritivores fed on conditioned and unconditioned litter and found that the only species with no higher growth on conditioned detritus was *S. vittatum*. One of the explanations given in their paper was that higher feeding rate of *S. vittatum* on low-conditioned litter would compensate for low food quality. Moreover, they emphasized the high feeding plasticity showed by some detritivores that allow them to grow using much differing diets. Such suggestion is in accordance with the results found by both FRIBERG and JACOBSEN (1999) with *S. personatum* and CARVALHO and GRAÇA (2007) with *S. vittatum*, who found that these *Sericostoma* species can use to grow leaf detritus differing in nutrient content and toughness, algae, fine detritus and aquatic macrophytes. We suggest that certain detritivore species, such as *S. vittatum*, may cope with foods of so much differing characteristics that include low-conditioned pine litter.

The results of our experiment indicate that the strategy of *S. vittatum* to obtain sufficient energy to grow when eating low conditioned pine litter was not compensatory feeding but to enhance production efficiency. GRAÇA (1994) discusses this strategy and names it maximization: when animals decrease the ingestion rates of poor quality detritus, they increase the gut passage times, maximizing nutrient and energy extracted per mass of ingested food (SIBLY, 1981). Maximization would be advantageous to assimilate food that is poor in easily digestible compounds because it extends the time for enzymatic hydrolysis of recalcitrant molecules.

#### 4.3. Is Pine Detritus an Adequate Food for Detritivores?

Another unexpected finding of this paper is that, contrary to previous literature on shredders feeding on conifers (e.g., GRAFIUS and ANDERSON, 1980; FRIBERG and JACOBSEN, 1994, 1999) and pine litter (e.g., ALBARIÑO and BALSEIRO, 2001, 2002; VALDOVINOS, 2001; COLLEN *et al.*, 2004), pine needles seem to adequately sustain growth in *S. vittatum* larvae, as found for other diets (Table 2). However, this capability should not be generalized for other shredders due to physiological inter-species variations (e.g., HERBST, 1982; ARSUFFI and

Table 2. Comparisons between the results of previous experiments on *Sericostoma* spp. growth ( $\text{day}^{-1}$ ) and the predictions made by the models constructed in this paper for animals fed on pine litter. As growth depends on larval mass, the predictions are made for the range of individual mass used in the experiments gathered from the literature.

Reference	Species	Individual mass (mg)	Food item	Observed daily growth ( $\text{day}^{-1}$ )	Results of this paper ( $\text{day}^{-1}$ ) for pine litter conditioned during:		
					4 weeks	8 weeks	30 weeks
FRIBERG and JACOBSEN (1999)	<i>S. personatum</i>	5.19 ± 0.47	<i>Potamogeton perfoliatus</i>	0.004	0.013–0.014	0.014–0.016	0.011–0.012
			<i>Picea sitchensis</i>	0.001	0.013–0.014	0.014–0.015	0.011–0.012
			<i>Alnus glutinosa</i>	0.007	0.014–0.017	0.016–0.018	0.012–0.014
			<i>Fraxinus excelsior</i>	0.007	0.015–0.016	0.017	0.013–0.014
			<i>Microspora</i> sp.	0.006	0.016	0.017	0.014
FEIO and GRAÇA (2000)	<i>S. vittatum</i>	3.8–10.5	<i>Castanea sativa</i>	0.036	0.003–0.016	0.005–0.018	0.002–0.014
GONZÁLEZ and GRAÇA (2003)	<i>S. vittatum</i>	3–5*	<i>A. glutinosa</i>	0.011–0.015	0.014–0.018	0.015–0.019	0.012–0.016
			<i>Castanea sativa</i>	0.006–0.010			
			<i>Populus x canadensis</i>	0.010–0.015			
			<i>Quercus andegavensis</i>	0.011–0.015			
CARVALHO and GRAÇA (2007)	<i>S. vittatum</i>	3.4–6.8	<i>powdered Alnus glutinosa</i>	0.046	0.010–0.017	0.012–0.019	0.009–0.015
			<i>A. glutinosa</i>	0.033			
			<i>Myriophyllum aquaticum</i> powdered <i>Acacia dealbata</i>	0.016 0.007			

\* GONZÁLEZ and GRAÇA (2003) report their results as a regression model between mass and daily growth. Arbitrary individual mass of 3 and 5 mg has been adopted for comparative purposes.

SUBERKROPP, 1986, 1989; MOTOMORI *et al.*, 2001; BJELKE and HERRMANN, 2005). In this context, FRIBERG and JACOBSEN (1994) found that *S. personatum* has less selective feeding than the detritivore amphipod *Gammarus pulex* and attributed its higher flexibility to (1) low mobility of the caddisfly, which makes the search for high quality food items more difficult (2) its large mandibles enabling it to use tough foods and (3) low respiration rate which makes a positive energy balance possible when eating low quality food.

In summary, this report highlights the difficulties to make generalizations on detritus use by macroinvertebrates. Our experiments have shown that the shredder caddisfly *S. vittatum* is able to transform pine needles into invertebrate production and that the microbial conditioning had an effect on feeding rates, but not on growth rate of this shredder. These results indicate that the commonly accepted idea that conifer detritus can only support shredder populations after a long time of microbial conditioning is not applicable to the entire guild.

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