



Consumption, growth and survival of the endemic stream shredder *Limnephilus atlanticus* (Trichoptera, Limnephilidae) fed with distinct leaf species



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ABSTRACT

Oceanic freshwater communities tend to be species poor but rich in endemism due to their physical isolation. The ecology of endemic freshwater species is, however, poorly known. This study assessed allometric relationships, feeding preferences, growth and survival of larvae of the endemic stream insect *Limnephilus atlanticus* (Trichoptera, Limnephilidae) exposed to four leaf species differing in their physical and chemical characteristics (*Ilex perado*, *Morella faya*, *Alnus glutinosa* and *Clethra arborea*), in laboratory trials. All regression models used to estimate *L. atlanticus* dry mass from body and case dimensions and wet mass were significant, but wet mass and body length were the best predictors. *Limnephilus atlanticus* consumed all the four leaf species offered, but when given a choice, shredders significantly preferred *A. glutinosa* over the other three leaf species. Relative larval growth rate was significantly higher when *L. atlanticus* fed on *A. glutinosa* and *I. perado* leaves in comparison with the other leaf species. Survival of 95% was found when individuals fed on *A. glutinosa* leaves while it decreased to 75% when they fed on the other leaf species. Our results suggest that *L. atlanticus* can be an active shredder and that it exhibits the same basic patterns of food exploitation as its continental counterparts. The lack of an effect of shredders on litter decomposition in Azorean streams revealed by previous studies may thus be due to low densities or to a preference for food resources other than the low quality native litter species.

1. Introduction

Organic matter derived from the riparian vegetation is a key source of energy for forest streams (Cummins et al., 1989; Wallace et al., 1997; Webster and Benfield, 1986). Once in water, this organic matter, generally in the form of leaf litter (Abelho, 2001), is decomposed by microbial decomposers and macroinvertebrate detritivores (Graça, 2001; Graça and Canhoto, 2006; Webster and Benfield, 1986). Microbes colonize leaf litter soon after leaf immersion and as microbial biomass accumulates the nutrient concentration in the litter increases (Gulis et al., 2006; Gulis and Suberkropp, 2003), which improves its nutritional value to invertebrate consumers (Graça, 2001; Graça and Cressa, 2010). Also, the activities of fungal exoenzymes promote leaf softening making feeding activities by invertebrates easier (Arsuffi and Suberkropp, 1989). In continental temperate streams, macroinvertebrate detritivores generally play an important role in leaf decomposition (Cornut et al., 2010; Gulis et al., 2006; Hieber and Gessner, 2002), while in islands leaf decomposition seems to be essentially driven by

microbes (Benstead et al., 2009; Ferreira et al., 2016; Raposeiro et al., 2014). The low contribution of the macroinvertebrate community to leaf decomposition in island streams may be related with the overall depauperate and disharmonic nature of the insular assemblages (Raposeiro et al., 2012; Smith et al., 2003).

The caddisfly *Limnephilus atlanticus* Nybom (1948) (Trichoptera, Limnephilidae) was described during the Finnish expedition to the Azores islands in 1938 (Nybom, 1948) and was found to be endemic of this archipelago. This taxon is known to be well distributed in the Azores archipelago (Borges, 2010; Raposeiro et al., 2012), especially in streams at high elevations flowing through native vegetation (Raposeiro et al., 2013). Because it belongs to the Limnephilidae family and has typical detritivore mouthparts, it is expected that this taxon be a shredder. Although shredders are less abundant and diverse in oceanic islands (Raposeiro et al., 2012) than in mainland streams, there is no a priori reason why insular shredders should have a feeding strategy much different from their continental counterparts. However, stream macroinvertebrate have little influence on the decomposition of

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leaf litter in insular freshwater ecosystems (Ferreira et al., 2016; Raposeiro et al., 2014). One possible explanation could be that most native plant species (e.g. Lauraceae, Aquifoliaceae) synthesize a large number of secondary substances that act as natural insecticide and likely diminish the palatability of the leaves to consumers (Rosa et al., 2010). Also, native species, especially the endemic ones, have a waxy cuticle and a thick palisade cell layer that protect the leaf mesophyll from consumers (Raposeiro et al., 2014).

Due to the difficulty of finding good quality leaves (i.e. soft with high nutrient concentration) in island streams, would *L. atlanticus* have adapted to poor quality food resources or is it using alternative food resources? The aim of this study was to determine whether *L. atlanticus* individuals use coarse organic matter as a food resource by assessing food preferences, consumption and growth rates and survival of *L. atlanticus* individuals fed with distinct leaf species.

2. Materials and methods

2.1. Collection of *Limnephilus atlanticus* larvae

Experiments were performed with early-stage larvae of *L. atlanticus*, a stream caddisfly endemic to the Azores archipelago and common in the upstream sections of some Azorean streams (Raposeiro et al., 2012, 2013). Individuals were collected in a single day from depositional areas in a first order reach of Ribeira do Folhado, São Miguel Island (37°48'48"N, 25°14'47"W; 729 m above sea level), in spring 2015, and transported to the laboratory in a cooler. Ribeira do Folhado is a narrow (1 m wide) and short (~7 km long) stream that drains an area < 10 km². Predominant substrates comprise mixed gravel/cobbles with occasional large, submerged boulders. The stream water is circumneutral, has low conductivity and low nutrient concentration (Table 1). The riparian forest is dominated by *Cryptomeria japonica* (L.f) D. Don and *Clethra arborea* Aiton trees.

2.2. Estimation of *Limnephilus atlanticus* dry mass

Individuals were maintained in plastic containers with aerated stream water and sediment, at 12 °C, and measured within 48 h after collection. Five case and body dimensions were taken with a stereomicroscope and used as predictors of biomass: case length (CL), case opening width (CW), body length (BL), head length (HL) and interocular distance (ID). Additionally, wet mass (body + case; WM) was determined after drying the individuals with paper (0.1 mg precision). Then, individuals were removed from their cases, placed individually in pre-weighed aluminum cups, dried at 60 °C for 24 h and weighed (0.1 mg precision) to determine the dry mass (DM). CW, BL and HL measurements were obtained for 74 larvae; CL, ID, WM and DM were obtained from 120 larvae.

Three regression models were used to determine the relationships between case and body measurements and DM. The data were fitted to the following models in order to determine which best described the relationship: linear ($y = a + b \times x$), power ($y = a \times x^b$; in linear

Table 1
Physical and chemical characteristics of Ribeira do Folhado between 2014 and 2015 (n = 5).

Water variables	Mean ± SE
Temperature (°C)	9.3 ± 0.3
pH	6.7 ± 0.4
Conductivity (µS/cm)	53.7 ± 3.1
Nitrate (µg NO ₃ ⁻ /L)	119.1 ± 21.6
Nitrite (µg NO ₂ ⁻ /L)	0.4 ± 0.4
Total nitrogen (µg N/L)	190.4 ± 36.3
Soluble reactive phosphorus (µg PO ₄ ²⁻ /L)	37.3 ± 11.5
Total phosphorus (µg P/L)	14.6 ± 44.9

form: $\ln(y) = \ln(a) + b \times \ln(x)$ and exponential ($y = a \times e^{bx}$; in linear form: $\ln(y) = \ln(a) + b \times x$), where y is DM (mg), x is case or body measurement (mm; mg for WM) and a and b are regression constants.

2.3. Leaves

Leaves from four tree species were used: *Ilex perado* Aiton and *Morella faya* Aiton are two native broadleaf perennial tree species commonly present in the riparian area of streams flowing through native vegetation, *Clethra arborea* Aiton is an invasive broadleaf perennial tree species also common in the riparian vegetation of Azorean streams, and *Alnus glutinosa* (L) Gaertn. is an exotic broadleaf deciduous tree species. *Alnus glutinosa* trees are rare in the Azores archipelago but previous studies have shown this to be a highly palatable leaf species to shredders (Friberg and Jacobsen, 1994; Graça and Cressa, 2010) and thus it was used here for comparative purposes. Leaves from the perennial species were collected directly from the trees since these shed leaves at a low rate, incompatible with the experimental needs for leaf litter. Alder leaves were collected after natural senescence in autumn. All leaves were transported to the laboratory where they were air dried at ambient conditions and stored in the dark until used.

Leaf species were characterized regarding toughness and chemical composition. Leaf toughness was determined using a penetrometer after leaves had been soaked in distilled water for 1 h and results were expressed as the force (g/mm²) needed to perforate the leaves with an iron rod (Graça et al., 2005). Subsamples of dry leaves were ground to fine powder (< 1 mm) and used for the determination of nitrogen (IRMS Thermo Delta V advantage with a Flash EA – 1112 series), phosphorus (Apha, 1995), lignin (Goering and Van Soest, 1970) and polyphenol concentration (Graça et al., 2005). Results were expressed as % DM. Comparison of physical and chemical characteristics among leaf species were done by one-way ANOVA, followed by Tukey's test.

Leaves were offered to individuals as 12 mm diameter leaf discs, extracted with a cork borer avoiding the main vein. Leaf discs were enclosed in 0.5 mm mesh bags (3.5 × 4.0 cm) and incubated for seven days in 25-L laboratory containers filled with water from Ribeira do Folhado that was continuously aerated. The water was renewed each 3 days to ensure the leaching of leaf soluble compounds and the colonization of leaf discs by microbial decomposers that increase litter palatability to shredders (Graça and Cressa, 2010; Graça et al., 2001). Discs were oven dried (60 °C for 48 h) and weighed (0.1 mg precision) to determine initial mass before being used in the experiments.

2.4. Experimental chambers

Experimental chambers consisted of 8.5 × 8.0 × 6.5 cm containers with 250 mL of filtered water (0.45 µm-pore membrane filter; GF/C, Whatman) and 10 g of ignited (8 h at 500 °C) sand (200 µm) from Ribeira do Folhado. Chambers were kept inside a Sanyo versatile Environmental Test Chamber, MLR-351-H (Japan), maintained at 12.0 ± 0.5 °C with a 10:14 h light:dark photoperiod, and aerated for the duration of the experiments. A single individual was weighed (WM; 0.1 mg precision) and added to each chamber. Larvae with similar size (40.0–50.0 mg) were selected to be used.

2.5. Feeding preferences

Limnephilus atlanticus were presented with: (i) a choice among the four leaf species, to provide a direct comparison of species preferences, and (ii) a no-choice situation with each leaf species being given individually. Twenty chambers were set up for the choice (total n = 20) and 40 chambers for the no-choice experiment (10 chambers × 4 species). In the choice experiment, each chamber received the four leaf species with the four leaf discs (one per leaf species) being

Table 2

Physical and chemical characteristics of the four leaf species used in the laboratory experiments (mean \pm SE). Different letters indicate significant differences (one-way ANOVA followed by Tukey's test, $P < 0.05$).

Leaf species	n	<i>A. glutinosa</i>	<i>C. arborea</i>	<i>I. perado</i>	<i>M. faya</i>
Force (g/mm ²)	10	56.81 \pm 4.56a	199.41 \pm 14.06b	564.91 \pm 13.23c	224.01 \pm 8.40b
Lignin (% DM)	3	35.79 \pm 0.38c	27.78 \pm 1.41b	22.38 \pm 1.43a	38.85 \pm 0.62c
Polyphenols (% DM)	3	3.52 \pm 0.26a	13.09 \pm 0.22c	6.63 \pm 0.23b	6.36 \pm 0.25b
Phosphorus (% DM)	3	0.14 \pm 0.01b	0.09 \pm 0.01a	0.07 \pm < 0.01a	0.06 \pm < 0.01a
Nitrogen (% DM)	3	2.48 \pm 0.10c	0.71 \pm 0.03a	0.80 \pm 0.02a	1.91 \pm 0.03b
Carbon (% DM)	3	47.47 \pm 0.96ab	45.07 \pm 0.56a	49.45 \pm 0.34b	49.85 \pm 0.17b

pinned in a circle near the boundary of the chamber, 2.5 cm apart. In the no-choice experiment, each chamber received a single leaf species with four conspecific discs being pinned in the center of the arena. Additionally, control chambers, similar to test chambers but without the individual, were set up to allow the estimation of leaf discs mass loss due to leaching and microbial activities in order to correct mass loss in test chambers for the loss due to leaching and microbial activity (Graça et al., 2005). The choice experiment ran until at least one of the exposed discs was consumed to half in at least one chamber, and the no-choice experiment ran until half of the discs were consumed in at least one chamber. Leaf discs (exposed and control) were oven dried (60 °C for 48 h) individually per species and weighed (0.1 mg precision) to determine remaining dry mass (DM).

The initial DM (mg) of each larva was determined from WM (mg) by the regression model $DM = -0.963 + 0.124 \times WM$ ($R^2 = 0.87$, $p < 0.001$). Relative consumption rate (RCR) was expressed as g leaf DM/g individual DM/day. Comparison among leaf species in the choice experiment was made using Friedman's test followed by the appropriate non-parametric post hoc comparisons (Wilcoxon Signed Rank Test). This test allows for comparing multiple non-independent treatments as long as replication equals or exceeds the number of treatments compared (Graça et al., 2005). Comparison of consumption among leaf species in the no-choice experiment was done using a one-way ANOVA model, followed by a Tukey post hoc test. Data were checked for heteroscedasticity (Cochran's test) prior to analysis.

2.6. Consumption, growth and survival

A similar experiment was carried out to assess *L. atlanticus* consumption and growth on each of the four leaf species. As we wanted to assess growth rate, this experiment lasted for 4 weeks. Ten microcosms were set up for each leaf species (total $n = 40$). Control microcosms with four discs of the same species and no individual were used to estimate mass loss that can occur in the absence of consumers. Every seven days, the sediment and water were replaced with freshly ignited sediment and filtered stream water, and the leaf discs (exposed and control) were sampled and replaced with newly conditioned leaf discs. Each group of four leaf discs was weighted at the start of each week and at the end discs (exposed and control) were oven dried (60 °C for 48 h) and weighted (0.1 mg precision) to determine remaining DM. At the end of the experiment larvae were also dried at 60 °C for 48 h and weighed (0.1 mg precision).

The initial DM of each larva was determined as described above. Relative consumption rates (RCR) were estimated for each feeding period as described above. Relative growth rates (RGR, mg DM/g DM/day) were estimated as $DMg/(DMf \times t)$, where DMg is the DM gained during the incubation period given by the difference between the initial and the final DM (mg) and DMf is the final DM (g) (Ferreira et al., 2010). Survival was determined as the percentage of individuals still alive at the end of the experiment. Comparison of consumption and growth rates over time among the four leaf species was done by two-way repeated measures ANOVA. Bonferroni's test was applied for post-hoc multiple comparisons.

3. Results

3.1. Leaves

The four leaf species selected differed in toughness and chemical characteristics (Table 2). *Alnus glutinosa* leaves were the softest and had the lowest polyphenols and the highest nutrient (both nitrogen and phosphorus) concentrations (Table 2). *Alnus glutinosa* and *M. faya* leaves had the highest lignin concentration (Table 2). *Morella faya* leaves had intermediate softness and intermediate polyphenols and nitrogen concentrations (Table 2). *Ilex perado* leaves were the toughest, had the lowest lignin concentration and low nutrients concentrations (Table 2). *Clethra arborea* leaves had intermediate softness and lignin concentration, the highest polyphenols concentration and low nutrients and carbon concentrations (Table 2).

3.2. Estimation of *Limnephilus atlanticus* dry mass

Limnephilus atlanticus larvae collected from Ribeira do Folhado varied in size and mass (Table 3). All regression models used to estimate *L. atlanticus* DM from body and case dimensions and WM were significant ($P < 0.001$). The best fit between body or case dimensions and DM was provided by the power models, followed by the exponential and the linear models (Table 4). WM – DM relationship was better fitted by the linear model ($R^2 = 0.87$), followed by the power ($R^2 = 0.86$) and the exponential model ($R^2 = 0.73$). DM was best predicted from WM ($R^2 = 0.73$ – 0.87 , across models) and BL ($R^2 = 0.78$ – 0.83) (Table 4). As the relationship between DM and WM was stronger than that between DM and BL for two out of three models, and WM is easier to determine on live individuals than BL, DM on experimental individuals was determined using the linear model DM – WM.

3.3. Feeding preferences

Limnephilus atlanticus consumed all four leaf species. When given a choice, relative consumption rates were in the order *A. glutinosa* > *I. perado* > *C. arborea* > *M. faya* (Fig. 1A), but significant differences were found only between *A. glutinosa* and the other three leaf species (Wilcoxon Signed Rank Test, $P < 0.005$). When individuals were given no choice, relative consumption rates were in the order *A. glutinosa* > *C. arborea* > *I. perado* > *M. faya*, with significant differences being found between *A. glutinosa* and *M. faya* (Tukey's test, $P = 0.01$) (Fig. 1B).

3.4. Consumption, growth and survival

Relative consumption rates significantly differed among leaf species (two-way repeated measures ANOVA, $P < 0.001$) and over the incubation period ($P = 0.019$). Litter consumption rates were relatively constant over time for *A. glutinosa*, *C. arborea* and *M. faya*, while it increased over the first three weeks for *I. perado* (Fig. 2A). Overall consumption rates were in the order *A. glutinosa* > *I. perado* > *C. arborea* > *M. faya*, but significant differences were found only be-

Table 3
Body and case dimensions and body mass of *L. atlanticus* larvae collected from Ribeira do Folhado.

Body dimensions and mass	Range	Mean	n
<i>Body dimensions (mm)</i>			
Body length (BL)	4.70–13.13	9.14	74
Interocular distance (ID)	0.07–0.80	0.22	120
Head length (HL)	0.86–1.86	1.50	74
<i>Case dimensions (mm)</i>			
Case length (CL)	6.13–14.75	10.7	120
Case width (CW)	1.50–3.40	2.55	74
<i>Body mass (mg)</i>			
Wet mass (WM)	6.70–93.50	32.34	120
Dry mass (DM)	0.10–12.20	3.47	120

Table 4
Linear, exponential and power models for the relationship between body and case dimensions (mm) and wet and dry mass (mg) of *L. atlanticus*. Dry mass (DM), wet mass (WM), interocular distance (ID), case length (CL), case width (CW), body length (BL), head length (HL).

Function	Models	a ± SE	b ± SE	R ²	n
<i>Linear</i>					
	WM – DM	−0.96 ± 0.17	0.12 ± 0.02	0.87	120
	ID – DM	0.93 ± 0.40	9.54 ± 1.56	0.24	120
	CL – DM	−5.15 ± 0.89	0.77 ± 0.09	0.43	120
	CW – DM	−7.89 ± 1.06	4.70 ± 0.42	0.65	74
	BL – DM	−6.70 ± 0.72	1.22 ± 0.09	0.78	74
	HL – DM	−4.95 ± 1.46	6.03 ± 0.96	0.36	74
<i>Exponential</i>					
	WM – DM	−0.62 ± 0.10	0.05 ± 0.01	0.73	120
	ID – DM	0.08 ± 0.17	3.38 ± 0.64	0.20	120
	CL – DM	−3.05 ± 0.29	0.36 ± 0.04	0.62	120
	CW – DM	−1.79 ± 0.24	1.20 ± 0.10	0.72	74
	BL – DM	−1.48 ± 0.17	0.30 ± 0.03	0.81	74
	HL – DM	−1.23 ± 0.33	1.66 ± 0.22	0.46	74
<i>Power</i>					
	WM – DM	−4.05 ± 0.20	1.46 ± 0.07	0.86	120
	ID – DM	2.47 ± 0.28	1.03 ± 0.17	0.25	120
	CL – DM	−8.11 ± 0.60	3.80 ± 0.26	0.67	120
	CW – DM	−1.52 ± 0.21	3.00 ± 0.22	0.73	74
	BL – DM	−4.77 ± 0.34	2.75 ± 0.16	0.83	74
	HL – DM	0.30 ± 0.14	2.44 ± 0.31	0.48	74

P < 0.001 for all models.

tween the first two and the last two species (Bonferroni post-hoc test, P < 0.010) (Fig. 3A).

Relative growth rates significantly differed among leaf species (two-way repeated measures ANOVA, P < 0.001) but did not significantly vary over time for any leaf species (P = 0.536) (Fig. 2B). Overall growth rates were in the order *A. glutinosa* > *I. perado* > *M. faya* > *C. arborea*, but were significantly higher when individuals fed on *A. glutinosa* and *I. perado* than on *M. faya* and *C. arborea* (Bonferroni post-hoc test, P < 0.050) (Fig. 3B). Survival was higher (95%) when individuals were fed on *A. glutinosa* leaves than when they were fed the other three leaf species (75%).

4. Discussion

The best predictors of dry mass for *L. atlanticus* larvae were wet mass and body length, explaining a maximum of 87% and 83% of dry mass variation, respectively. Body length has been found to be a good predictor of dry mass for aquatic insect larvae in many previous studies (e.g. Benke et al., 1999; Burgherr and Meyer, 1997; Johnston and Cunjak, 1999; Meyer, 1989; Smock, 1980). However, our results suggested that wet mass is an equally good predictor of dry mass for *L. atlanticus* larvae. Also, it is advantageous to use wet mass over body length to estimate dry mass in studies using live case-building organ-

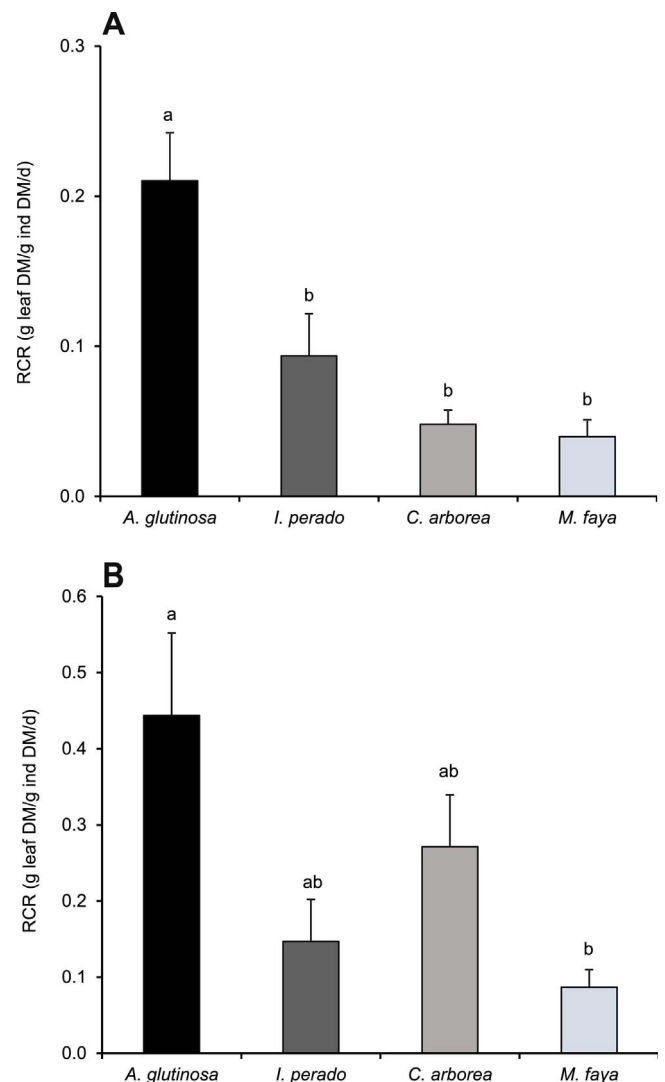


Fig. 1. Leaf litter consumption (mean ± SE) by *L. atlanticus* individuals fed with *A. glutinosa*, *I. perado*, *C. arborea* and *M. faya* leaves, when shredders were given a choice (four leaf species available) (A) and when shredders were fed on individual leaf species (B). Different letters indicate significant differences (Wilcoxon Signed Rank (A) and Tukey test (B), P < 0.05).

isms. These organisms have to be removed from their cases for body length measurement, which is time consuming and has a higher risk of stressing the organisms and breaking body structures compared with determination of wet mass (body + case).

It is widely accepted that shredders, including *Limnephilus* spp., feed preferentially on certain leaf types based on their physical and chemical characteristics with soft leaves with high nutrient concentration generally being preferred over tough leaves (Canhoto and Graça, 1995; Cronin et al., 1998; Leberfinger and Bohman, 2010; Swan and Palmer, 2006). In agreement, *L. atlanticus* larvae, when given a choice, preferred *A. glutinosa* leaves over the others leaf species (*I. perado*, *C. arborea* and *M. faya*), suggesting that this endemic shredder has feeding preferences similar to its mainland counterparts. When individuals did not have a choice, consumption rate was higher on *A. glutinosa* leaves than on *M. faya*. Feeding preferences of *L. atlanticus* can be explained by the intrinsic characteristics of the leaves.

Alnus glutinosa leaves were the softest and had the highest nutrient concentration, and the lowest concentration of polyphenols, making it a palatable substrate for *L. atlanticus*. On the other hand, *M. faya* had the highest lignin concentration and was tough. Surprisingly, consumption on *I. perado*, when it was offered individually, was not significantly

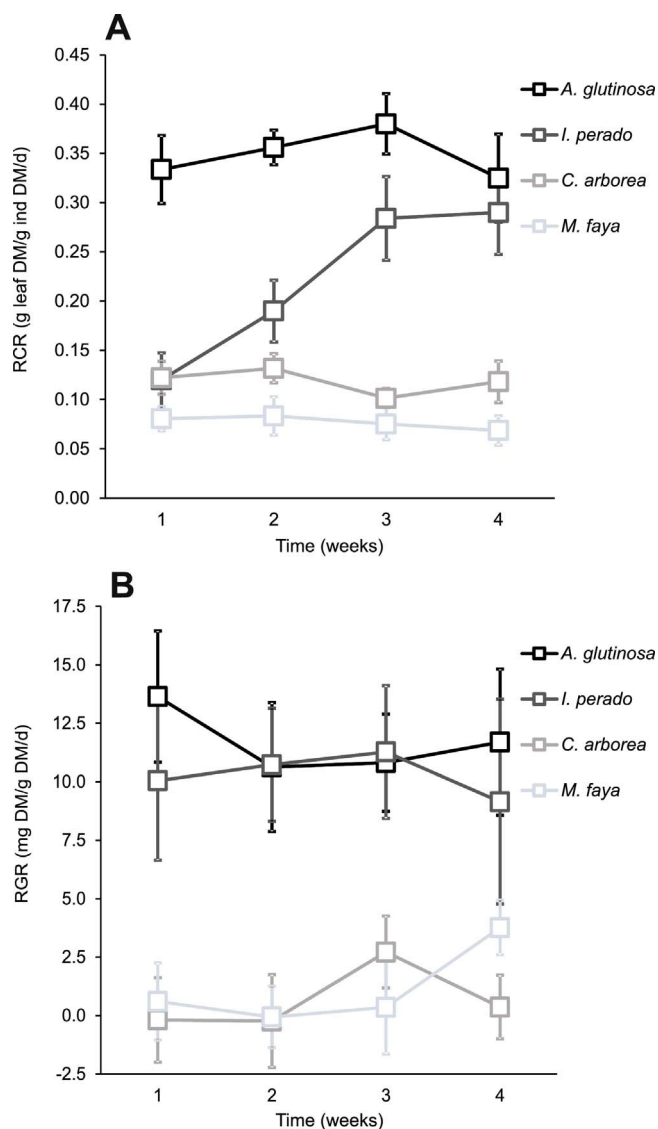


Fig. 2. Relative consumption rate (RCR; A) and relative growth rate (RGR; B) (mean \pm SE) of *L. atlanticus* individuals fed with *A. glutinosa*, *I. perado*, *C. arborea* and *M. faya* leaves over four weeks.

different from that observed on *A. glutinosa* despite *I. perado* being the toughest leaf species and having low nutrient concentration. However, in *I. perado*, the tough cuticle detached from the leaf mesophyll during incubation and larvae could directly assess the mesophyll overcoming the potentially inhibiting effect of the tough cuticle. This suggests that leaf toughness is a key leaf characteristic determining shredder feeding, as observed before (Graça and Cressa, 2010). This agrees with previous studies that suggest that litter toughness and the concentration of structural compounds may be more important than nutrient concentrations in determining biological colonization and litter decomposition rates (Li et al., 2009; Schindler and Gessner, 2009). Thus, *L. atlanticus* preferred soft leaves with low concentration of lignin and polyphenols and high nutrient concentration, showing a similar feeding behavior to other Trichoptera species (Rincón and Martínez, 2006).

In the four weeks experiment, consumption rates by *L. atlanticus* varied between 0.05–0.35 g leaf DM/g individual DM/day and were in the range observed previously for other shredders (*Triplectides* sp.: Casotti et al., 2014; *Sericostoma vittatum*: Ferreira et al., 2010). Ranges of growth rates were higher in our study (0.5–12.0 mg ind DM/g ind DM/day) compared to those obtained for *S. vittatum* in a similar laboratory experiment (Ferreira et al., 2010; 6.0–8.0 mg ind DM/g

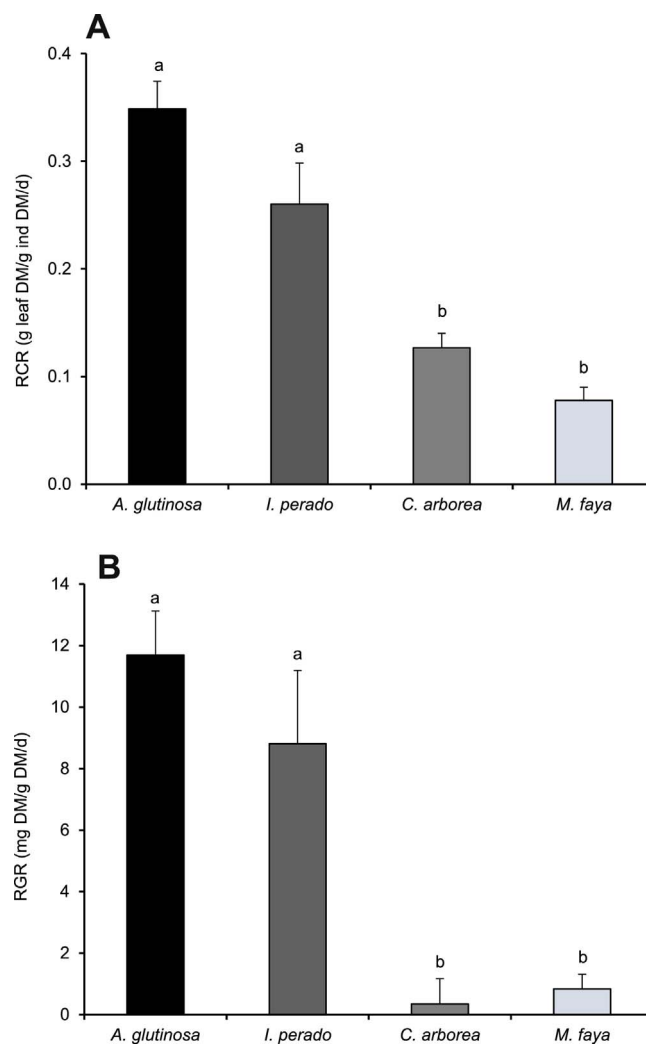


Fig. 3. Relative consumption rate (RCR; A) and relative growth rate (RGR; B) (mean \pm SE) of *L. atlanticus* individuals fed with *A. glutinosa*, *I. perado*, *C. arborea* and *M. faya* leaves. Different letters indicate significant differences (Bonferroni test, $P < 0.05$).

ind DM/day) likely due to the stronger differences in leaf quality among leaf species in our study.

Limnephilus atlanticus had higher consumption and growth rates when fed *A. glutinosa* or *I. perado* than when fed *C. arborea* or *M. faya*, which are explained by differences in food quality. As discussed above, *A. glutinosa* was the best quality leaf species. Although *I. perado* leaves did not have such a high nutrient concentration as *A. glutinosa*, shredders experienced a similar consumption and growth. *Ilex perado* had lower concentration of polyphenols and lignin that may have facilitate its digestibility and therefore larval growth (note that the higher toughness was alleviated by the cuticle detaching from the leaf mesophyll). Previous studies have shown that high growth rates not only occur with a high nutrient concentration, but that other intrinsic leaf properties such as texture or secondary compounds may affect digestion and thus influence growth (Carvalho and Graça, 2007; Friberg and Jacobsen, 1999). Also, previous studies have shown that shredders may exhibit compensatory feeding by which they compensate for lower food quality by increasing their consumption rates (Arsuffi and Suberkropp, 1989; Iversen, 1974).

Survival of *L. atlanticus* was higher (95%) when individuals fed on *A. glutinosa* than when they fed on the other leaf species (75%). *Alnus glutinosa* is well known as a high-quality resource for stream detritivores (Canhoto and Graça, 1995; Friberg and Jacobsen, 1994; Graça and Cressa, 2010), while the other three species have secondary compounds

that may be toxic.

Our results suggest that *L. atlanticus* can act as an active shredder and that it exhibits the same basic patterns of food exploitation as its continental counterparts. Although, macroinvertebrates generally play a key role in leaf litter decomposition in temperate aquatic streams in continental habitats (Graça and Canhoto, 2006), recent studies (Ferreira et al., 2016; Raposeiro et al., 2014) found that macroinvertebrates had no major effect on litter decomposition in Azorean streams, and that leaf litter decomposition was driven by microbial activity.

Similar results on the low importance of macroinvertebrates on litter decomposition were found in streams with low abundance of shredders in tropical islands as Hawaii and eastern Caroline Islands (Benstead et al., 2009; Larned, 2000). However, when shredders are present, litter decomposition in island streams can be stimulated over that observed due to microbial activity only (Crowl et al., 2006; Larned et al., 2003; Rincón and Covich, 2014; Wright and Covich, 2005a,b). Macroconsumers in particular (e.g. decapods) have been shown to highly contribute to litter decomposition in tropical island streams (Wright and Covich, 2005a,b; Crowl et al., 2001, 2006). The lack of shredder influence in litter decomposition in Azorean streams may be explained by the fact that predominant riparian vegetation is composed by hard leaf species with low nutrient concentration. In this condition, shredders may return to alternative food sources since their feeding plasticity is well known (Carvalho and Graça, 2007; Friberg and Jacobsen, 1994). The role these organisms play in island stream ecosystems is still unclear.

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