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Grazing impact of two aquatic invertebrates on periphyton from an Andean-Patagonian stream

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With 6 figures and 4 tables

Abstract: The mayfly *Meridialaris chiloeensis* and the snail *Chilina dombeiana* were observed to coexist and develop abundant populations in several Andean streams. In this study we examined and compared the mouthpart morphologies and the grazing mechanisms of these two species. In addition, through field experiments we analysed the grazing effect on periphyton composition and biomass. Results showed that the herbivores contrasted in their mouthpart morphology and foraging behaviour but would play a similar ecological role, since they both can be considered as scrapers. Experimental results indicated that the individual mayfly effect on chlorophyll-a and ash free dry mass was lower than that of the individual snail. However, considering the spring and autumn abundances of both populations in a natural environment, their grazing impact might be similar or even higher for the mayfly. In addition, *M. chiloeensis* depressed the rosette forming algae and favoured the prostrate ones. As a result, the mayfly grazing produced a community dominated by *Nitzschia palea* instead of *Achnanthes minutissima* that dominated the grazer-free controls, while the snail changed the taxonomic composition very little.

Key words: *Meridialaris chiloeensis, Chilina dombeiana,* coexistence, mouthpart morphology, scrapers.

Introduction

Snails and mayflies are important benthic primary consumers in many streams (Lamberti 1996), affecting periphyton species assemblage, biomass and productivity (Feminella & Hawkins 1995). In low order streams, the periphyton that grows on stony surfaces is grazed mainly by scrapers, with mouthparts

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adapted to reach tightly attached algae, by brushers, who use setae to dislodge periphyton, and by gathering-collectors, that use structures other than setae to gather lightly attached or loosely deposited organic material (McShaffrey & McCafferty 1988). As a result of grazing, periphytic biomass decreases and upright algal species are often reduced, whereas small and prostrate species are favoured (Sumner & McIntire 1982, Hill & Knight 1987, Karouna & Fuller 1992, Feminella & Hawkins 1995). In classical models, algal physiognomy and herbivore feeding mode regulate algal susceptibility to grazing (Steinman 1996). Nevertheless, Wellnitz & Ward (2000) achieved results that contradict model predictions, suggesting that understanding periphytic community responses to grazing will require more sophisticated models of periphytic structure.

Snails of the genus *Chilina* and mayflies of the genus *Meridialaris* constitute an important fraction of the aquatic fauna in streams from the Andean-Patagonian region (Castellanos & Gaillard 1981, Domínguez et al. 1994). *Meridialaris* (Ephemeroptera: Leptophlebiidae) is endemic to Argentina and Chile, and *M. chiloeensis* (Demoullin) is restricted to the Southern Andes (Pescador & Peters 1987). Pulmonate snails of the genus *Chilina* (Basommatophorida: Chilinidae) are also endemic to South America, preferring the cold Andean waters (Castellanos & Gaillard 1981). In particular, *Chilina dombeiana* (Bruguiere) inhabits streams and lake shores (Castellanos & Gaillard 1981) and is commonly associated with large stony substrate.

The two grazers *M. chiloeensis* and *C. dombeiana* coexist and are very abundant in some Andean streams (Domínguez et al. 1994, Castellanos & Gaillard 1981). The objective of this study was to examine and compare the mouthpart morphologies and the grazing mechanisms of these two species. We performed two field experiments to contrast the effects of these two species on periphyton composition and biomass, and to evaluate if and how these grazers partition periphyton to facilitate coexistence.

Methods

Study area

Meridialaris chiloeensis and *Chilina dombeiana* coexist in Gutiérrez stream (41° 07′ S and 71° 25′ W, Argentina). This stream flows through an open valley of fluvioglacial origin, from Lake Gutiérrez (785 m a. s. l.) into Lake Nahuel Huapi (764 m a. s. l.), with a slope of 4 m km^{-1}. The flow velocity varied between 23 and 96 cm s^{-1}. At the sampling site, the stream is 6 m wide and the bottom has a boulder-cobble substrate. The stream has a flow regime dominated by rainfall in fall and snowmelt in spring, with minimum discharge in late summer. Stream conductivity is extremely low, varying between 20 and 40 µS cm^{-1}. Chemical composition of South Andean rivers and streams is dominated by calcium, bicarbonate and dissolved silica (Pedrozo et al. 1993). This stream contains a diverse fish assemblage dominated by salmonids (Díaz Villanueva et al. 2000).

Field study

Herbivore abundance in Gutiérrez stream was estimated in autumn (April) and spring (October) 2000 from a 30 m stream section in riffle habitats, located 6 km from Lake Gutiérrez. Ten Surber samples (0.09 m^2 and 200 μm mesh size) were taken and invertebrates were preserved in 10 % formalin. In the laboratory, *M. chiloeensis* and *C. dombeiana* were separated and counted under a stereomicroscope. They were dried at 80 °C for 24 h and weighed to the nearest 0.1 mg. Then, they were combusted at 550 °C for 3 hours and re-weighed. The ash free dry mass (AFDM) was estimated as the difference in mass before and after incineration.

The periphyton was analysed in the autumn sampling from five randomly selected stones (10–15 cm diameter) collected in the same stream section. Substrates were carried to the laboratory individually in plastic containers and in darkness. The stone surfaces were brushed with a toothbrush and rinsed with distilled water and the total volume was collected. A subsample of 25 ml was filtered through Whatman GF/C filters in order to estimate periphyton biomass as Chlorophyll-a concentration (Chl-a). Chlorophyll-a was extracted with hot ethanol 90 % following Nusch (1980) and measured with a fluorometer (AU 10, Turner). Stone surface area was estimated by covering the brushed area with aluminium foil and then by measuring this area using Image-Pro Plus 4.5 (Media Cybernetics). Algae biomass was expressed as Chl-a concentration ($\mu g\ cm^{-2}$). Algal species composition was studied from the remaining volume of the brushed periphyton, preserved in 4 % formalin and observed in a Sedgwick-Rafter chamber of 18 μl under a microscope at 400 × magnification. A 10 ml subsample was treated with hydrogen peroxide to oxidise organic matter and it was used to identify and count diatoms. Percentages of species abundance were determined based on counts. The slides were mounted in Naphrax® and examined at 1000×. Identifications were performed according to Krammer & Lange-Bertalot (1986, 1988, 1991).

Laboratoy study

M. chiloeensis mouthparts and *C. dombeiana* radulae were examined under a stereomicroscope and dissected. They were dried in absolute ethanol for observation under a scanning electronic microscope (Philips 515).

Some animals were kept alive for feeding observations. Mouthpart movements of the two herbivores were observed directly while feeding on periphyton. Individuals were placed in rearing chambers with aerated, filtrated water and starved for 24 h. Afterwards, the specimens were introduced to Petri dishes with a transparent plastic sheet (5 × 5 cm) that was colonised by natural periphyton in Gutiérrez stream for 20 days prior to the start of the experiment. The mouthpart movements were observed while the grazers were kept upside down feeding on the periphyton layer of the transparent plastic sheet. Aerated water was provided by a peristaltic pump and organisms were left to acclimatise 5 minutes before observations. Feeding observations were made under a stereomicroscope (50×) using red light. A feeding activity sequence was recorded using an image analyser (Image Pro, Media Cybernetics).

Experimental design

In Experiment 1, we examined how the two herbivores affected periphyton community biomass and species composition. This experiment was carried out between 29 September and 13 October 1998 in a single streamside channel at the Centro de Salmonicultura beside Gutiérrez stream. The channel consisted of a 400×40×40 cm fibreglass structure and was fed with Gutiérrez stream water. Water level was maintained at 14 cm depth with a discharge of 25.8 l min^{-1}. Temperature was 11 ± 1 °C during the experiment. Experimental units consisted of unglazed ceramic tiles (8×8 cm) as substrates for periphyton growth and grazing. The tiles were covered by transparent Plexiglas half pipe that shaped a semicircular tunnel, with both ends closed with a net of 1 mm mesh.

On 29 September, fifteen experimental units were placed in the channel for periphytic colonisation. After one week, grazers were collected from the stream and placed in the enclosures separately, resulting in three treatments: *M. chiloeensis*, *C. dombeiana*, and a control without grazers. Each treatment and the control were run in four replicates (4 enclosures each). Equivalent biomass of the two grazers (22.6 ± 4.5 mg AFDM) was placed in each chamber. This condition was achieved with five mayflies or one snail per enclosure. This design would have induced a high grazing pressure, since grazers were constrained to 64 cm^2. When the herbivores were introduced, 3 chambers were collected to measure the initial periphyton biomass. Herbivores were left to graze for 7 days and then all tiles were transported to the laboratory in darkness. Grazers were killed with hot water and immediately dried, weighed, combusted and reweighed in order to quantify their biomass.

In the laboratory, the tiles were scraped with a razor-blade and rinsed with 90 ml distilled water. The periphyton samples were carefully homogenised and fractionated into three subsamples of 30 ml, in order to determine biomass as Chl-a, ash free dry mass (AFDM), and species composition and cell abundances. Chl-a was estimated as was previously described, although measurements were carried out with a spectrophotometer at 665 nm and 750 nm, and corrections for pheophytin were performed after acidification with HCl (Nusch 1980). Subsamples for periphyton AFDM determinations were filtered onto preweighed and precombusted Whatman GF/C filters and dried at 80 °C for 1.5 h. The filters were weighed, combusted at 550 °C for 1 h and reweighed to determine AFDM (APHA 1989).

In order to compare the grazing effect on periphyton physiognomy, we grouped the diatom species in five categories according to their growth habits, following Roemer et al. (1984), Katho (1992) and Kutka & Richards (1996). The categories considered were: adnate, prostrate, rosette forming, filamentous and arborescent.

The difference in the proportion of a diatom species on the controls and each treatment was assumed as the proportion of that species that was eaten by each herbivore (pi). The food niche overlap was calculated using the Pianka index (Pianka 1974):

$$\Theta = \frac{\sum P_{i1} \cdot P_{i2}}{\sum P_{i1}{}^2 \cdot P_{i2}{}^2} \qquad \text{Equation 1}$$

where p_{i1} is the proportion of ith food category in the diet of species 1; p_{i2} is the proportion of this category in the diet of species 2. This index varies from 0 to 1, the values of 0.5–1 pointing to high overlap, below 0.5 to niche separation.

In Experiment 2, we analysed temporal variation of the grazing effect of the two herbivores on periphytic biomass. The experiment was conducted between 7 September and 9 October 2000 at the Centro de Salmonicultura beside Gutiérrez stream. In this experiment, we used 9 channels (experimental units) with a row of 10 ceramic tiles (8 × 8 cm) placed inside. The channels were constructed of PVC and were 1.5 m long and 0.1 m wide. The channel's ends were covered with a net of 1 mm mesh and fed with Gutiérrez stream water at a rate of $7\,l\,\mathrm{min}^{-1}$. Tiles were left to colonise with periphyton for one month. The grazers were not constrained to the upper surface of the tiles, to allow the grazers to use the underside of the tiles as a spatial refuge.

Treatments were the same as in Experiment 1 (*M. chiloeensis* and *C. dombeiana* separately) and controls consisted of channels without grazers. There were three replicates for each treatment. After 30 days of colonisation, 40 mayflies and 16 snails were introduced into each channel creating densities of 800 and 300 individuals m^{-2}, respectively. At that time and after 4, 8, 16 and 32 days, two tiles per channel were collected, periphyton was removed and Chl-a and AFDM determined.

Removal rates (R) were calculated both for periphyton Chl-a concentration and AFDM as follows:

$$R = \frac{C - G}{D \cdot H} \qquad \text{Equation 2}$$

where C is the final Chl-a concentration or AFDM in controls, G is the same variable in each treatment, D is the total time in days and H is the grazer abundance or total biomass in each treatment (Cattaneo & Mousseau 1995). This rate includes not only consumed material but also sloughed periphyton (Lamberti et al. 1987).

Statistical differences in periphyton biomass in Experiment 1 were analysed with one-way ANOVA and the effects of both grazers on the different algal categories with two-way ANOVA. Normality and homocedasticity were tested using Kolmogorov-Smirnov test (Zar 1999). The proportions of diatom categories were transformed applying arcsine $\sqrt{p}$ (Zar 1999). In Experiment 2, temporal variation in periphyton biomass was compared with two-way repeated measurement ANOVA (Zar 1999). Tukey's test was used for *a posteriori* multiple contrasts. Chlorophyll-a data were log-transformed. Removal rates of *M. chiloeensis* and *C. dombeiana* were compared with t-test (Sokal & Rohlf 1981).

Results

Field study, mouthpart morphology and feeding movements

Meridialaris chiloeensis and *Chilina dombeiana* were present on both sampling occasions (Table 1). In autumn, the population of *M. chiloeensis* consisted of small larvae (0.27 ± 0.08 mg of individual AFDM and 1.00 ± 0.05 cm of total length) representing 29 % of the total macroinvertebrate density and

Table 1. Total invertebrate and grazer abundances in riffle habitats of Gutiérrez stream. Values represent individuals (abundance) or biomass (mg of ash free dry mass) per m^{-2}. Values are mean ± 1 S. E.

Herbivores	Autumn (May)		Spring (October)	
	Abundance	Biomass	Abundance	Biomass
Meridialaris chiloeensis	457±183	125± 40	66± 9	101± 19
Chilina dombeiana	184± 43	829±189	32± 3	163± 40
Total Macroinvertebrates	1583±310	1956±311	2253±127	964±139

Table 2. Percentage of diatom species (relative abundance >0.1) found in the periphyton from Experiment 1 (control, *M. chiloeensis* and *C. dombeiana* treatments) and Gutiérrez stream. Growth habit references: R: rosette forming; F: filamentous; P: prostrate; A: adnate; PN: pedunculate.

	habit	Control	*Meridialaris*	*Chilina*	stream
Achnanthes minutissima KÜTZ.	R	19.78	11.07	19.74	34.10
Fragilaria capuchina DESM.	F	16.52	16.10	11.99	6.81
Nitzschia palea (KÜTZ.) W. SMITH	P	14.89	24.24	14.24	0.05
Nitzschia linearis (AG.) W. SMITH	P	7.54	10.05	6.91	0.00
Fragilaria pinnata EHR.	F	6.58	5.56	5.92	3.50
Cyclotella stelligera CL. & GRUN.	P	6.16	6.38	9.57	2.12
Cocconeis placentula EHR.	A	4.02	3.61	5.32	8.20
Cymbella silesiaca BLEISH	PN	3.08	4.06	2.65	6.94
Navicula sp1	P	2.06	1.00	0.80	0.00
Nitzschia recta HANT.	P	2.06	2.82	2.62	0.00
Achnanthes pusilla KÜTZ.	A	2.02	0.64	1.50	1.85
Gomphonema angustatum AG.	PN	1.91	2.40	2.03	13.27
Synedra ulna (NITZ.) EHR.	R	1.61	1.93	2.29	2.86
Fragilaria bicapitata MAYER	F	1.46	3.16	1.89	1.38
Navicula cryptocephala KÜTZ.	P	1.41	0.62	1.26	0.62
Melosira varians AG.	F	0.87	1.15	1.26	10.42
Gomphoneis minutum KOC. & STR.	PN	0.50	1.08	0.84	1.13

7 % of total macroinvertebrate biomass. However, in spring these values changed to 3 % and 11 %, respectively, after adult emergence reduced the larvae abundance but development increased individual biomass. On the other hand, *C. dombeiana* was found in low abundance but with a high contribution to total macroinvertebrate biomass (42 % in autumn and 11 % in spring).

In autumn, the periphytic Chl-a concentration was of $1.17 \pm 0.18\,\mu g\ cm^{-2}$ (mean ± s. e.). Diatoms dominated the epilithic algal assemblage and the most abundant species were *Achnanthes minutissima* KÜTZ., followed by *Gomphonema angustatum* AG. and *Melosira varians* AG. (Table 2).

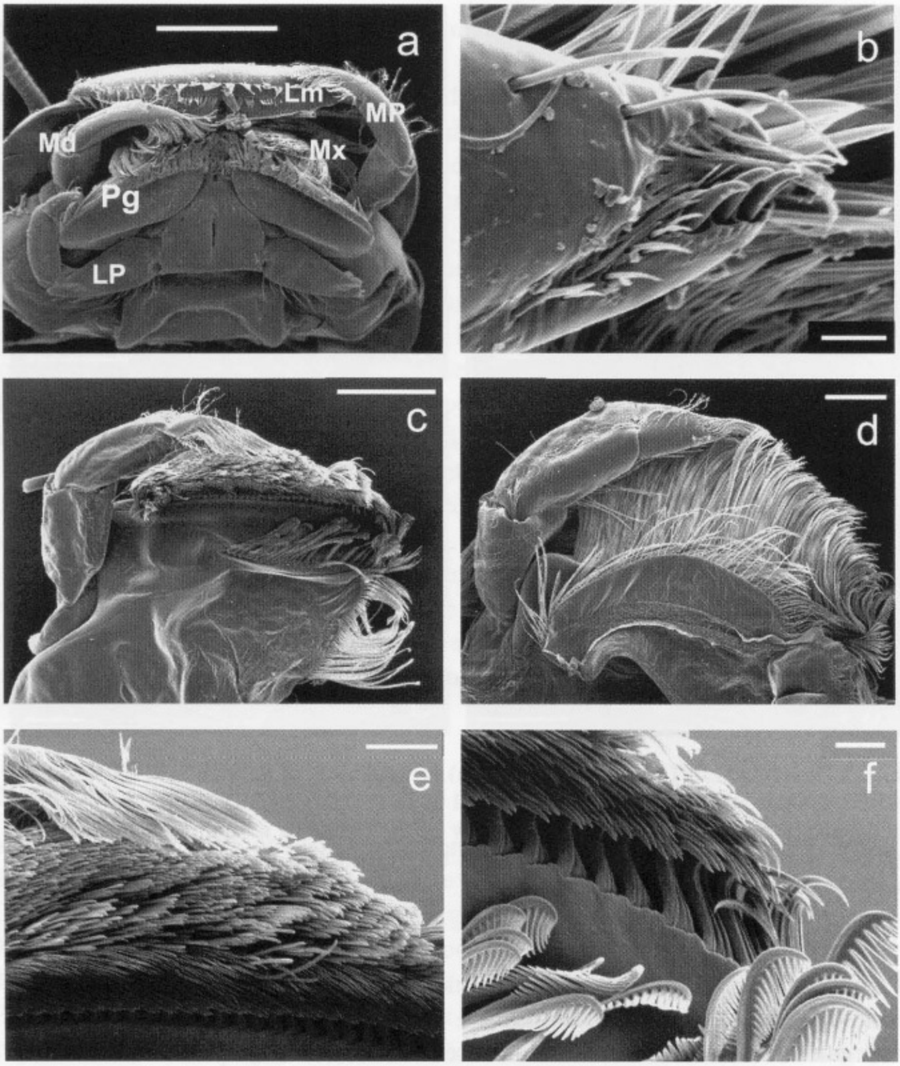

Fig. 1. Mouthparts of *Meridialaris chiloeensis.* **a)** ventral view of the mouthparts. Lm: labrum, Md: mandible, Mx: maxilla, MP: maxillary palp, Pg: paraglossa, LP: labial palp, scale bar 400 µm; **b)** tip of labial palp, scale bar 10 µm; **c)** right maxilla (lacinia-galea and palp) in ventral view, scale bar 200 µm; **d)** left maxilla and superlingua in dorsal view, scale bar 100 µm; **e)** detail of maxillary brush in ventral view, scale bar 50 µm; **f)** apical bristles of the maxillary brush in ventral view, scale bar 20 µm.

Mouthparts of *M. chiloeensis* are characterised by bearing a large number of bristles of different morphologies. The labium has very small glossae and wide and flattened paraglossae (Fig. 1 a). Both structures bear moderately short and bipectinate bristles (length: 58.3 ± 2.7 µm, width: 2.2 ± 0.1 µm) at the apex.

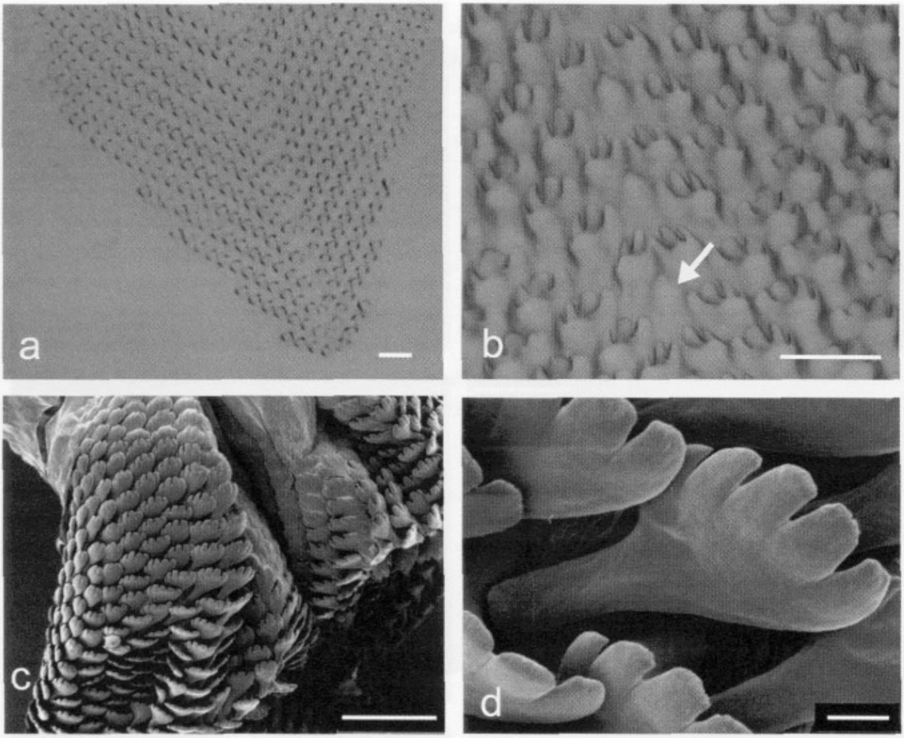

Fig. 2. Mouthparts of *Chilina dombeiana.* **a)** general view of the radula in optic microscope, scale bar 100 µm; **b)** detail of central teeth showing raquideous (arrow) and lateral teeth, scale bar 50 µm; **c)** general view of the radula in scanning electron microscope showing its teeth arrangement, scale bar 100 µm; **d)** detail of one lateral tooth, scale bar 10 µm.

Labial palps are three-segmented and the apical one bears a set of few short hairs at the tip (Fig. 1 b). Maxillae are the most complex structures. Lacinia and galea are fused into a wide and stout structure. The apex of the lacinia-galea is wide, straight and very sclerotized (Fig. 1 c). It has a dense brush with two types of stout bristles (Fig. 1 c–f). The ventral ones are short (length: 46.6 ± 3.6 µm, basal width: 6.2 ± 0.4), simple and hook-like, forming a tight band (Fig. 1 e, f). The dorsal ones become gradually longer and less dense (length: up to 480.0 µm, width: 2.6 ± 0.2 µm) and they are bipectinate (Fig. 1 d, e). Maxillary palps are long and stout structures with an apical brush of long bipectinate bristles (length: 146.9 ± 9.4 µm; width: 1.5 ± 0.1 µm; Fig. 1 a, c, e). Mandibles are large and sclerotized structures with slender incisors and a reduced inner molar area.

The direct observations indicated that the animals begin feeding by extending the maxillae and maxillary palps laterally. The head remains in prognathus position forming a slight angle (approximately 30°) with the substrate. Immediately afterwards, both pairs of palps and maxillae are laterally extended, moved down against the substratum and retracted inwards, brushing material from that surface. Simultaneously, labial palps are laterally extended and retracted opposite to maxillae. These structures work together in handling the dislodged food. After a brushing maxillary cycle is completed, both mandibles and maxillae are raised and moved apart, probably producing a current into the mouth. This cycle is repeated several times before moving to another place.

Chilina's radula consists of numerous oblique rows of teeth, all similar to each other (Fig. 2 a–c). The radula has 1.7 10^3–2.6 10^3 teeth per mm^2. Each tooth is connected to the basal membrane through a stem, which becomes wider to the apex forming a denticulate lobe (Fig. 2 d). Denticle morphology and number change gradually from sharp and less denticulate (three pointed) in the centre (Fig. 2 b) to blunt and multi-denticulate (4–5 points) in the margins (Fig. 2 c). Tooth size ranges from 21.6 to 36.8 μm width and 35.5 to 55.1 μm length.

Snail foraging behaviour was different from that of the mayfly. *C. dombeiana* fed while crawling, spreading the radula on the substratum, dragging it across the substrate surface and immediately ingesting the dislodged periphyton. The radula was then retracted into the mouth and then it was spread again to initiate another cycle.

Experimental study

In Experiment 1, after one week of colonisation, diatoms dominated the epilithic algal assemblage, comprising more than 83 % of total algal abundance. Chl-a concentration was of 0.16 ± 0.03 μg cm^{-2} (mean ± s. e.) and, AFDM was 0.06 ± 0.01 mg cm^{-2}. After 7 days of exposure to grazers, we found significant differences between the two treatments and the control (ANOVA, $P < 0.05$; Fig. 3). Both species caused a significant reduction in periphyton biomass (Tukey test, $P < 0.01$) (Fig. 3 a, b). The effect on Chl-a concentration was very similar for both grazers (Tukey test, $P > 0.05$), although the mayfly reduced AFDM more effectively than the snail (Tukey test, $P < 0.05$).

Diatom abundances were depressed on the tiles exposed to grazers (ANOVA, $P < 0.05$; Fig. 3 c); nevertheless, there were no statistical differences between the two species (Tukey test, $P > 0.05$; Fig. 3 c). Diatom species number decreased as a consequence of *M. chiloeensis* grazing from 41 in the controls to 34 in the mayfly treatments (Tukey test, $P < 0.05$), but it did not change in the snail treatments (Tukey test, $P > 0.05$).

Pianka's index obtained for *M. chiloeensis* and *C. dombeiana* was 0.12, indicating that the food niche of these species did not overlap. However, algal species composition changed differentially during this experiment. In controls,

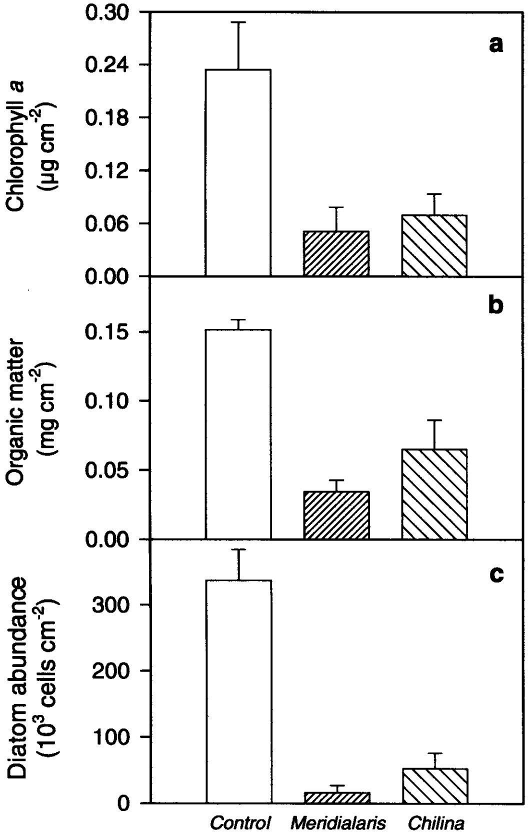

Fig. 3. Periphytic biomass in Experiment 1. **a)** Chlorophyll-a concentration, **b)** Organic matter as ash free dry mass, **c)** Diatom abundance (Error bar = 1 standard error).

Table 3. Summary of the two-way ANOVA comparing diatom habit and grazers in Experiment 1. DF: degree of freedom, MS: mean square.

Factor	DF	MS	F-ratio	p
Growth habit	4	0.2999	83.2901	<0.0001
Grazers	2	0.0008	0.2318	0.7941
Growth habit X Grazers	8	0.0113	3.1298	0.0067
Error	45	0.0036		

the algal assemblage was dominated by *Achnanthes minutissima* (20 %) and *Fragilaria capuccina* Desm. (15 %). In the *M. chiloeensis* treatment, the dominance changed towards *Nitzschia palea* (Kütz.) W. Smith while *A. minutissima* was the species most negatively affected (Table 2). The grazing effect of the snail on the diatom assemblage was restricted to *F. capuccina,* which was

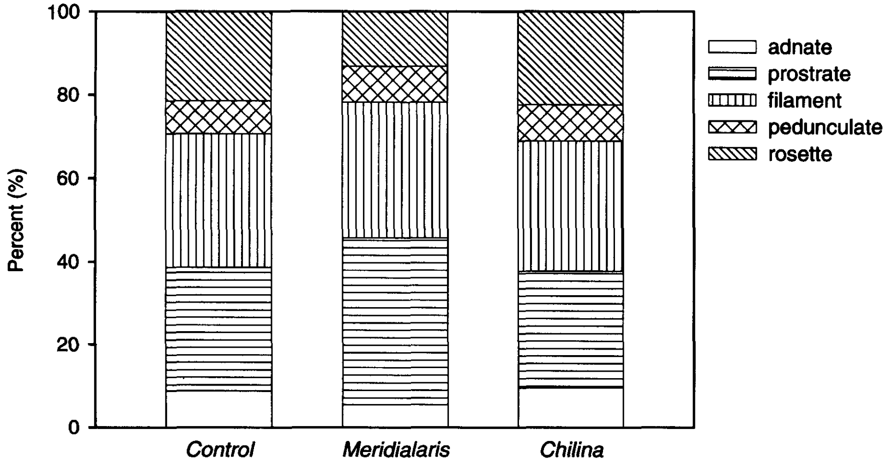

Fig. 4. Relative abundance of the diatom habits in the periphyton in Experiment 1.

Table 4. Summary of the two-way repeated measures ANOVA comparing grazers and time of exposition in Experiment 2. DF: degree of freedom, MS: mean square.

Factor	DF	MS	F-ratio	p
Chlorophyll-a				
Grazers	2	11.5522	3.9118	0.0338
Date	3	7.2759	2.4638	0.0869
Grazers X Date	6	2.1852	0.7399	0.6228
Error	24	2.9532		
AFDM				
Grazers	2	5.0523	11.6569	0.0003
Date	3	2.1164	4.8840	0.0086
Grazers X Date	6	1.5506	3.5784	0.0112
Error	24	0.4333		

reduced in relative abundance (Table 2). Consequently, the mayfly's grazing produced a significant difference in the periphyton physiognomy (two way-ANOVA, $P < 0.05$, Table 3, Fig. 4). Prostrate diatoms became more abundant and rosette forming diatoms became less abundant (Tukey test, $P < 0.05$). By contrast, the snail did not produce a significant difference in algal assemblage from that of the control (two way-ANOVA, $P > 0.05$, Table 3, Fig. 4).

In Experiment 2, Chl-a was $1.47 \pm 0.09\,\mu\text{g cm}^{-2}$ after 30 days of colonisation, and this value was very close to that measured in the stream. After the herbivores were introduced in the channels, periphytic biomass was significantly affected by the two herbivores (two way repeated measures-ANOVA, $P < 0.05$, Table 4). Periphytic Chl-a and AFDM increased until day 16 in both

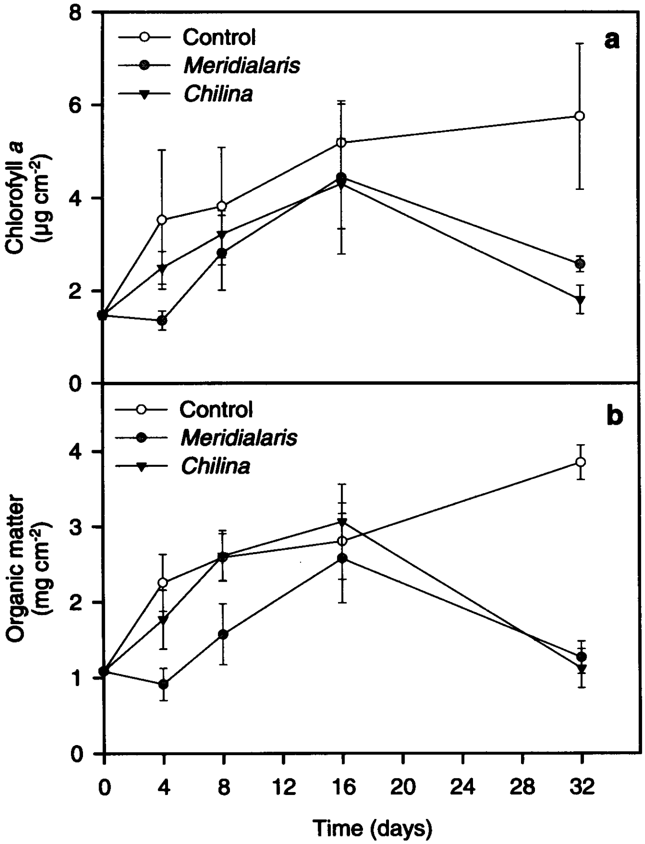

Fig. 5. Periphytic biomass variation during Experiment 2. **a)** Chlorophyll-a concentration; **b)** organic matter as ash free dry mass. (Error bar = 1 standard error).

treatments and control (Fig. 5), and at day 32 herbivores reduced periphyton (Tukey test, $P < 0.05$) and no differential impact of the two species was observed (Tukey test, $P > 0.05$) (Fig. 5).

This experiment allowed us to observe different patterns in the foraging behaviour of the two herbivores. *Meridialaris chiloeensis* cleaned up the surface near the borders of the tiles showing a clear dependence on the underside. By contrast, *Chilina* was commonly found on the tile surfaces during day and its behaviour consisted of wandering, leaving recognisable pathways on the tiles. On some occasions, the paths tunnelled inside the periphytic mat, and caused large patches of the mat to become detached.

Removal rates, in terms of Chl-a concentration or AFDM *per* individual, were higher for *C. dombeiana* than for *M. chiloeensis* (t-test, $P < 0.05$; Fig. 6 a). Conversely, when calculated per herbivore biomass, *M. chiloeensis*

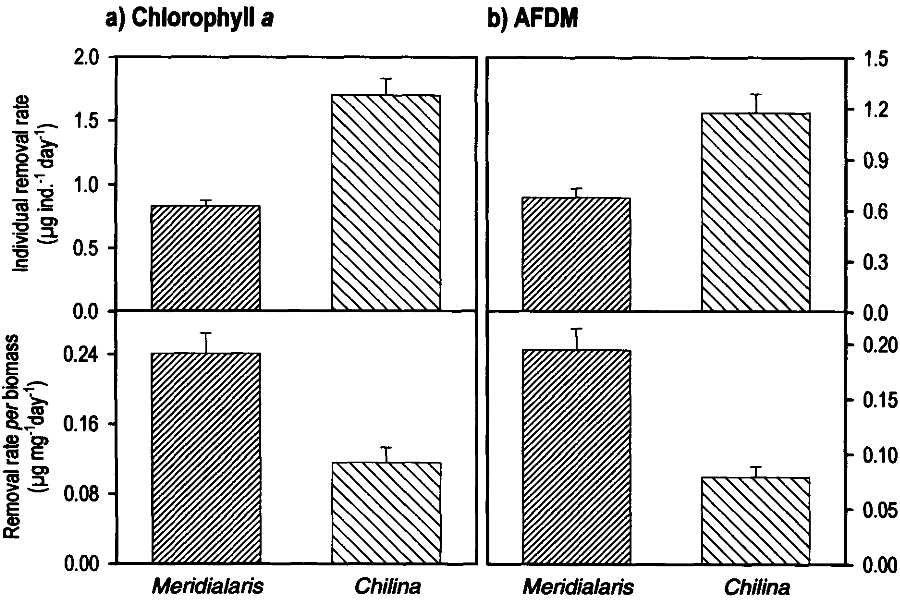

Fig. 6. Removal rates calculated for both herbivores in Experiment 2. **a)** Chlorophyll-a removed per individual; **b)** organic matter removed per individual; **c)** Chlorophyll-a removed per herbivore biomass; **d)** organic matter removed per herbivore biomass. (Error bar = 1 standard error).

removal rate was more than two fold that of *C. dombeiana* (t-test, $P < 0.05$; Fig. 6 b). Based on *C. dombeiana* and *M. chiloeensis* abundances in Gutiérrez stream, we estimated periphyton removal rates for each grazer using Equation 2. In spring the mayfly and the snail removed 44 mg m^{-2} d^{-1} and 37 mg m^{-2} d^{-1} respectively; in autumn, removal rates were 308 mg m^{-2} d^{-1} and 216 mg m^{-2} d^{-1}.

Discussion

In Gutiérrez stream, the mayfly *M. chiloeensis* and the snail *C. dombeiana* play a similar ecological role, since they can be considered as scrapers. However, considering the Gregory-Steinman model (STEINMAN 1996), the mayfly might be better classified as a scraper and gatherer whereas the snail would be a scraper and rasper.

Leptophlebiid mayflies have characteristic maxillary brushes that allow them to exploit the organic layer on stones (PALMER et al. 1993). In particular, *M. chiloeensis* maxillary brushes (lacinia-galeae and palps) were found to be the main structure used to obtain food. MCSHAFFREY & MCCAFFERTY (1988) proposed that the Heptageniid *Rhithrogena pellucida* combines both brushing and scraping cycles by using different mouthparts, being a scraper when it uses the ventral-brush of its maxillary palps. Likewise, *M. chiloeensis* presents a ventral band of short and hook-like bristles, which is probably involved in scraping activity. The scraping use of the galealacinial brush was also suggested by POLEGATTO & FROEHLICH (2001) for the Brasilian Leptophlebiid *Farrodes* sp. In addition, the ability of *Meridialaris* to access more tightly attached algae (*Achnanthes* spp.) may also indicate a scraping function of their maxillae.

In contrast to *M. chiloeensis* brushing mouthparts, *C. dombeiana*'s radula possesses a high density of equal sized teeth (hologlosan radulae) arranged in homogeneous rows that make it a very efficient scraping structure. Snails are mentioned to have higher grazing effects relative to other periphyton herbivores (STEINMAN 1996). Prosobranch and pulmonate snails differ in their radula structures, the former distinguished by having a central tooth and lateral teeth (CASTELLANOS 1994). In particular, lotic prosobranchs have considerably greater impact on periphyton than pulmonates (FEMINELLA & HAWKINS 1995).

Most grazing experiments that compare more than one species have examined widely different grazer population densities or biomasses, thereby the effects of individual taxa and abundance have been confounded (FEMINELLA & HAWKINS 1995). So, when comparing effects produced by two different species, it is necessary to take into account both their density and biomass. Our experimental results indicated that the individual mayfly effect was lower than that of the individual snail. This is consistent with the results obtained by LAMBERTI et al. (1987, 1995) for mayflies and snails. However, considering the spring and autumn abundances of both populations in Gutiérrez stream, their grazing impact might be similar or even higher for the mayfly.

In our experiments, the grazing impact of *M. chiloeensis* and *C. dombeiana* on periphyton biomass was found to be equivalent. Nevertheless, both species were observed to have a very low food niche overlap (Pianka index = 0.12). These contrasting results may suggest that periphyton would be affected in different ways. Many authors (SUMNER & MCINTIRE 1982, LAMBERTI & RESH 1983, LAMBERTI et al. 1989, ROSEMOND et al. 1993) have observed that grazing influences algal community structure, both taxonomically and physiognomically. Mayflies have usually been observed to feed on upright algal species (SUMNER & MCINTIRE 1982, HILL & KNIGHT 1987) and to exert low effect on periphyton relative to other grazers (FEMINELLA & HAWKINS 1995). In our experiments, *M. chiloeensis*, had a relative high impact on periphyton, depressing the rosette forming algae and favouring the prostrate ones. The repeated brushing maxillary cycle described in our direct observations would largely contribute to access to the thin organic layer. As a whole result, the mayfly grazing produced a community dominated by *N. palea* instead of *A. minutissima* that dominated the controls, while the snail changed the specific composition very little. This pattern may indicate that algal physiognomy is a poor predictor of vulnerability to consumers as was indicated by WELLNITZ & WARD (2000). Also some diatom species were observed alive in the faeces of *Meridialaris* larvae in laboratory experiments (DÍAZ VILLANUEVA & ALBARIÑO 2003), suggesting a possible indirect enhancement of these algae by nutrient uptake during gut passage.

In Gutiérrez stream, mayflies and snails shared epilithic algae as food resources and they may have an impact on ephiliton physiognomies as was observed in our experiments. In addition, our Experiment 2 allowed us to determine that *M. chiloeensis* and *C. dombeiana* had different spatial patterns in the foraging behaviour. These differences in grazing behaviour may also occur in natural environments, since snails were frequently seen exposed on stone surfaces during daytime while mayflies were not. Therefore, the coexistence of these species might be also due to differential uses of the microhabitat.

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